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EDITORS :—

Dr C. D. DARLINGTON
John Innes Institution
Bayfordbury, Hertford, Herts.

Prof. R. A. FISHER
Whittingehame Lodge
Cambridge

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INTRA-SPECIFIC DIFFERENTIATION IN *GOSSYPIUM HIRSUTUM*

J. B. HUTCHINSON

Empire Cotton Growing Corporation Cotton Research Station, Namulonge, Uganda

Received 22.ii.51

I. INTRODUCTION

THE taxonomy of the lint-bearing cottons has been greatly simplified in the past twenty-five years, and only five species are now recognised in this section of the genus *Gossypium*. Much of the variation formerly regarded as inter-specific has consequently been included within the species. While some of this variation is no more than random heterogeneity within the lowest recognisable taxonomic units, an important part of it is not randomly distributed, but so assorted between different parts of the range as to give rise to distinct geographical races. Some of these are readily identified, and have been given varietal names, but the less distinct are only recognisable with confidence in extensive collections of material representative of the whole range of the species. Such a representative range has been studied in *G. arboreum* by Silow (1944). He concluded that geographical factors had dominated intra-specific differentiation, but that the geographical races so formed were generally highly variable, and consequently not sufficiently distinct to justify a formal taxonomic sub-classification. Recently (Hutchinson, 1950), Silow's interpretation of intra-specific differentiation has been shown to be applicable to *G. herbaceum* as well as to *G. arboreum*, and it is now apparent that in all the cultivated species of *Gossypium*, sub-specific differentiation is best treated in terms of geographical distribution.

Sub-specific differentiation in the cottons is small relative to that between species. There is good evidence that it is of recent origin, and the barriers between the races are rarely complete, and usually allow of some gene interchange between them. Hence morphological differences are generally small, and it is often impossible to assign a single specimen to a particular race unless its place of origin is known. Nevertheless, when a large collection is assembled and is grouped according to localities, the relationship between types from the same area is clear, and it is possible to divide the range into areas between which there are consistent distinctions.

It has long been accepted that the centre of variability of *G. hirsutum* is in Central America, but in the absence of adequate collections from that region, classification has perforce been based on material

from the peripheral areas of its distribution. The species is at present divided into the typical form and two varieties. Accounts of the typical form are heavily weighted by data from the commercial Upland stocks of the American Cotton Belt. The description of var. *punctatum* was based on West African material, and until recently the New World *punctatums* have been regarded as of only secondary interest. The separation of var. *marie-galante* followed studies of West Indian cottons, with some reference to collections from Ecuador, the Spanish Main and Brazil. In no recent discussion save that of Mauer (1930) has any range of Central American material been considered. This can now be remedied, as extensive collections have recently been made in Mexico and Guatemala by Richmond (in 1945-46), Stephens (in 1946-47) and Ware and Manning (in 1948). The area traversed by these collectors lies between the Mexican States of Guerrero and Puebla to the west, and the Republic of El Salvador to the east. The Pacific coast was better covered than the coast of the Gulf of Mexico, but a small collection of Gulf coast types was provided by Dr I. Kelly. Collections from north of Mexico City would be of interest, and material from Honduras, Nicaragua and Panama is desirable to link up the Central American cottons with the *marie-galantes* of Colombia, but the Mexican and Guatemalan accessions cover the most important part of the Central American range. A very large proportion of the material collected belongs to *G. hirsutum*. Forms of *G. barbadense* were found occasionally throughout the area, but they showed little variability apart from the distinction between free and kidney seed, and they will not be considered further in this paper.

The system of collection was in general to take seed from any distinct lot of cotton that was observed. A few accessions from coastal Guatemala represent small samples of seed from ginneries, and a few more were obtained in country markets. A considerable number were from pickings of representative plants in small field crops. The great majority, however, were obtained from occasional plants or groups of plants in house yards, field margins, or hedgerows. In general, therefore, an accession may be taken to represent the interest in cotton of a single household, rather than any particular unit of the cotton population. The number of accessions available from an area, in fact, reflects the time spent by the collectors in the area, and only indirectly the density of its cotton population.*

The new material is of great taxonomic interest. It exhibits on

* Dr Stephens comments: "This is definitely incorrect in my case at least. There was absolutely no correlation. I collected more in a single day from certain regions, than in many days in others. In Salvador one really had to comb to find any cottons at all. Quite the opposite situation in Yucatan. I think one could say that the number of collections was definitely proportional to the density of the population in the sampled area; even more—that the relatively small areas sampled were representative of the larger natural regions in which they occurred."

the one hand a diversity that is not contemplated in the current classification of the species (Hutchinson, 1947), and on the other, an orderly differentiation that is not discernible among the multiplicity of species proposed in earlier works. A reassessment of the species is therefore necessary, and division into seven geographical races is proposed. The perennial varieties *punctatum* and *marie-galante* as at present understood constitute two of these races. Four of the others are also perennials, and to these the names *yucatanense*, *morrilli*, *richmondi*, and *palmeri* will be given. The seventh, and most important, is made up of the generally annual group to which the Upland cottons belong. To this the name *latifolium* (from *G. latifolium* Murray) seems appropriate. Three of the races, *punctatum*, *marie-galante* and *latifolium*, have spread further than the rest, and have undergone further differentiation, but apart from the consequences of their wider distribution and greater agricultural success, they are in no way different in rank from those that are confined to Central America.

The intra-racial differentiation of *latifolium* is of the greatest agricultural importance. It commenced in Central America, where the early fruiting forms spread through areas occupied by previously differentiated perennial races, and has continued in the vast extensions of range which *latifolium* has enjoyed in post-Columbian times. It can now be seen in progress in the United States Cotton Belt, and in India and Africa. This most recent, and continuing, differentiation is the process with which the plant breeder is concerned, and an understanding of it, and of the conditions by which it is governed, will make possible better planning of his work.

2. THE GEOGRAPHICAL RACES OF *G. HIRSUTUM*

The classification of the races of *G. hirsutum* is based on three seasons' observations on living material grown in the Sudan and Uganda. Richmond's and Stephens' collections were grown at Shambat (near Khartoum in the Sudan) in the 1947-48 season, when a preliminary classification was made. In the 1948-49 season they were grown again, one complete set of plots being sown early (beginning of July), and a second set late (mid-August). Seed of the Ware-Manning collection was received in August 1948, and sown immediately after the second sowing of the other series. The whole of the *latifolium* section of the C.R.S. collection * was grown at Namulonge in Uganda in the 1949-50 season, and the discussion on the distribution of variability given later in this paper was developed with constant reference to this material in the experimental plots.

As the classification proceeded it became evident that the collections made on the three separate expeditions gave a remarkably consistent

* The C.R.S. collection is the world collection of cottons and cotton relatives maintained by the research stations of the Empire Cotton Growing Corporation. It is now located at Shambat, near Khartoum, in the Sudan.

picture of the distributions of the seven races. Each of the six perennial races has its own distinct area in which it is practically the sole perennial type to be found, and outside which it occurs rarely if at all. A certain amount of overlap, with consequent blurring of the racial distinctions by intercrossing, occurs at the margins, but the areas of overlap are only a small proportion of the whole. The annual *latifolium* has spread widely in recent years, but when the regions in which it is known to be a recent introduction are omitted, the presumably primitive area of the race fits into the pattern formed by the rest. The distributions of the races are discussed in more detail later, but they may be summarised here for convenience.

The most northerly race is *morrilli*. It is dominant on the Mexican plateau in Oaxaca, Puebla and Morelos, and from earlier collections (Cook and Hubbard, 1926) is known to extend as far north as Sonora and Sinaloa. *Palmeri* is the sole perennial race in the State of Guerrero and in the neighbouring coastal region of western Oaxaca, and has only been collected occasionally elsewhere. *Richmondi* is confined to a small area on the south coast of the Isthmus of Tehuantepec, with a few outliers on the edge of the plateau in Oaxaca, and in Chiapas. To the east, *marie-galante* is the native perennial of coastal Guatemala and El Salvador eastwards from Escuintla, presumably linking through Costa Rica and Panama with its better known area of distribution on the Spanish Main.

TABLE 1

Distribution by Races of Accessions of G. hirsutum *from Central America*

Area	Race						
	morrilli	*richmondi*	*palmeri*	*punctatum*	*yucatan-ense*	*marie-galante*	*lati-folium*
Sonora and Sinaloa	3	...	...	...	...	...	...
Puebla and Morelos	9	...	1	...	...	...	...
Oaxaca	71	5	...	...	...	...	11*
Guerrero and W. Oaxaca	...	...	49	...	...	...	20*
Salina Cruz (Isthmus of Tehuantepec)	...	8	...	...	...	...	...
Chiapas	...	4	2	6	...	...	31
Peten (N. Guatemala)	...	...	...	23	...	...	...
Yucatan and Campeche	...	...	2	29	12	...	...
Central Guatemala	...	...	...	8	...	...	90
S. Coastal Guatemala	...	...	...	...	...	...	29
E. Guatemala and El Salvador	...	...	...	...	...	30	...

On the north coast of Central America, race *punctatum* is distributed in British Honduras and northern Guatemala, and in all the Gulf coastal states of Mexico, particularly in Yucatan. The specialised race *yucatanense* is confined to coastal sand dunes in north Yucatan.

Race *latifolium* is the cotton of central Guatemala and the Motagua valley, spreading west into Chiapas, and (in recent years) into Oaxaca and Guerrero.

These distributions are summarised in table 1, and are outlined in the map given in fig. 1. Extensions of the range of race *latifolium* that are known to have taken place recently are starred in the table, but are omitted from the map.

Plant habit characters provide the most important distinguishing features of the races of *G. hirsutum*. As they were almost always obscured in the old and often mutilated house yard and hedgerow

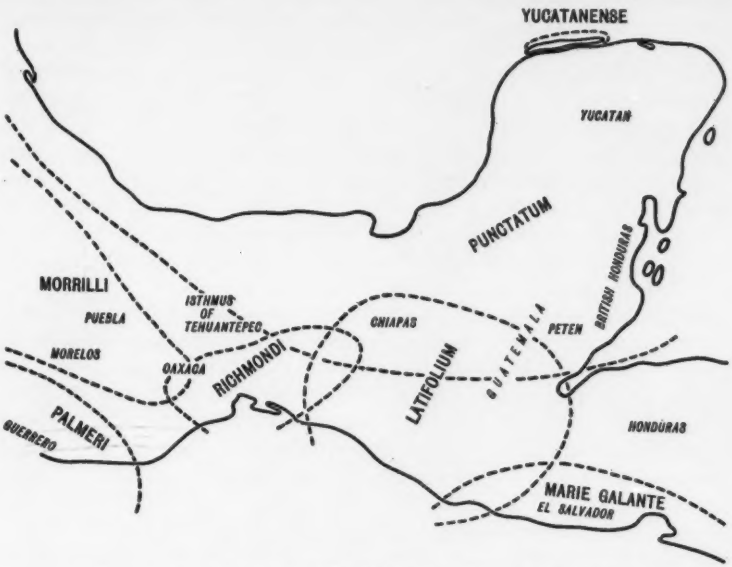

FIG. 1.—The Central American Distribution of Races of *G. hirsutum*.

plants * which provided seed of most of the accessions, field notes were of no assistance in classification, and the account given below is based entirely on observations on young and well-grown plants in the experimental plots. Though this material was strictly comparable, it did not, of course, represent anything more than response of the genotypes to the climates of the northern Sudan and Uganda. The morphological differences between races were much the same in these two widely different climates, however, and the comparisons may therefore be regarded as valid.

* Dr Stephens comments: "This is quite correct as regards Upland and *punctatum* types. . . . I do not feel happy at the placement of *marie-galante* as an equal subdivision with the other races. A novice can easily pick out *marie-galante* from the rest—he would be hard put to it to distinguish the others in the field."

Habit is a complex of many correlated characters, and it is not easy to sum up. An attempt was made to assess its more important components under size and general growth form, nature and development of vegetative branches, type of stem (rigidity and internode length), and node at which the first sympodial fruiting branch arose. An important, but less easily distinguished, habit character is the photoperiodic control of fruiting. This has been studied by Konstantinov (1934), who has summarised his conclusions as follows : "... the cotton plant should be ranked among plants of the short day. ... The earliest and early forms do not answer to shortening of the day ; intermediate forms exhibit a slight reaction. The shortening of the day exerts the strongest effect upon the perennial arboreous cottons ; there are forms belonging to this group, however, which nevertheless do not react or react slightly to the shortening of the day. The basic change that is produced in the cotton plant by shortening of the period of illumination consists in lowering of the level at which the first fructiferous branch is formed." The node number of the first fruiting branch, and the number of vegetative branches formed were recorded on all material, and an estimate of photoperiodic response was obtained by comparing data from plots sown in early July with those from plots sown in mid-August (1948-49 crop at Shambat). The latitude of Shambat is about 16° N., about the same as that of central Guatemala, and the difference in day length was not large. Other environmental differences were small also. There was very little rain in July, and none thereafter, and the irrigation rotation was the same for both sowings. Humidity dropped from August onward, but there was no great drop in temperatures until November. Nevertheless, very striking differences were recorded between the two sowings in both node number and number of fruiting branches (see table 4). The difference between early and late sowings is simply termed sowing date response, but in view of Konstantinov's findings it is probable that the causative factor was in fact day length.

Information on seed cotton and lint characters was collected as opportunity offered, having regard to the first requirement from plots of all collections, which was the provision of adequate self-bred seed for future use. In the 1948-49 season, fuzz type and fuzz colour were recorded on all types, and lint colour and lint length (measured as halo length in mm.) on most. Ginning outturn was determined on those that gave sufficient seed cotton, either selfed or open pollinated. Since self pollination reduces the number of seeds per boll in some strains, the weight of seed cotton per boll was only determined on types from which sufficient naturally pollinated bolls were picked. The characteristics of the seven races are summarised in tables 2 and 3. Habit characters, as being most important, are given first, followed by leaf, stem and boll characters that often provide useful ancillary distinguishing marks. Mean values for lint and seed characters are also included, though their range of variation is in

general so great as to provide little of value in distinguishing the races. Detailed data on sowing date response are given in table 4, and on lint and seed characters in tables 5-8.

TABLE 2

The characteristics of the races of G. hirsutum
(Central American accessions only)

Character	*morrilli*	*richmondi*	*palmeri*
Habit characters			
Size and general growth form	large, upright, perennial shrubs	large, lax, sprawling perennial shrubs	compact, upright, perennial shrubs
Vegetative branches	10-20, ascending, often overtopping the main stem	10-20, long lax, spreading	15-20, ascending, considerably shorter than the main stem
Stems . . .	stiff and erect	flexible, internodes long	stiff and erect, internodes short
1st sympodial node	17-32	13-22	20-30
Sowing date response (see table 4)	strong	considerable	considerable
Leaf, stem and boll characters			
Stem tip and leaf hairiness	densely hairy, hairs short	glabrous or nearly so	glabrous or nearly so
Leaves . .	⅓ to ⅔ cut	⅓ to ⅔ cut	palmatifid, rarely lanceolate entire
Leaf lobes . .	divergent, tapering	divergent, tapering	divergent, lanceolate acuminate
Stem anthocyanin	weak or absent	weak or absent	strong
Bolls . . .	round, not opening widely	round, opening widely	round, opening widely
Seed cotton per boll	*c.* 1·5 gm.	*c.* 3·0 gm.	*c.* 1·5 gm.
Lint and seed characters			
Mean lint length .	*c.* 27 mm.	*c.* 30 mm.	*c.* 27 mm.
Lint colour . .	white, creamy, grey or brown	creamy	creamy, rarely brown
Ginning outturn (per cent.)	*c.* 26	*c.* 26	*c.* 30
Seed type . .	fuzzy	fuzzy	fuzzy
Fuzz . . .	green	green, greenish or brownish	green, rarely brown

The differences between the early and late sown progenies in both node number and number of vegetative branches (table 4) are very striking. The two characters are strongly correlated, and there are also strong correlations between the data from the same strains at the two sowing dates. Differences between sowing dates are small in the low node number types, and large in those with high node numbers, thus matching the day length effect reported by Konstantinov (1934).

The range of lint length and ginning outturn is large in all races. In the whole series of collections the upper limit of lint length is low, only 42 plants (10 per cent. of the whole) having given mean lengths over 30 mm. In ginning outturn on the other hand, high values are common. Even in the perennial races ginning outturns of 32 per

TABLE 3

The characteristics of the races of G. hirsutum (*Central American accessions only*)

Character	*punctatum*	*yucatanense*	*marie-galante*	*latifolium*
Habit characters				
Size and general growth form	bushy perennial shrubs	small, slow-growing perennial sub-shrubs	large perennial shrubs or small trees	annual sub-shrubs, sometimes persisting for 2 years
Vegetative branches	8-15, spreading or prostrate	many, prostrate	8-20 spreading or slightly ascending, not overtopping the main stem	0-5, spreading or ascending
Stems	flexible, bowing under the crop	prostrate	stout and upright	usually upright, sometimes sprawling
1st sympodial node	14-20	...	20-30	8-10
Sowing date response (see table 4)	considerable, except in early Chiapas form	...	strong	slight or absent
Leaf, stem and boll characters				
Stem tip and leaf hairiness	sparse or nearly glabrous	nearly glabrous	glabrous, sometimes moderately hairy	glabrous, sparsely or densely hairy
Leaves	very shallowly cut	very shallowly cut	$\frac{1}{3}$ to $\frac{2}{3}$ cut	$\frac{1}{3}$ cut or less
Leaf lobes	parallel- sided	parallel-sided	divergent, tapering	divergent, broadly triangular
Stem anthocyanin	moderate to strong	slight	usually slight, sometimes strong	usually slight
Bolls	oval or round, opening widely	very small, round, opening widely	round or oval, opening widely	round, oval or long, opening widely
Seed cotton per boll	*c.* 1·8 gm.	...	*c.* 1·7 gm.	2·0-6·3 gm.
Lint and seed characters				
Mean lint length	*c.* 27 mm.	*c.* 20 mm.	*c.* 25 mm.	*c.* 27 mm.
Lint colour	white, often brown in Yucatan	grey or medium brown	white, dull, grey, or light brown	white, creamy, light or rusty brown
Ginning outturn (per cent.)	*c.* 28	*c.* 20	*c.* 32	28-38
Seed type	fuzzy or tufted	fuzzy	fuzzy, tufted or naked	fuzzy or tufted
Fuzz	white, brown on brown linted types	brownish	green, sometimes brownish	white, green or brown

cent. and upwards were not uncommon, and in *latifolium* the Oaxaca, Guerrero and Chiapas field crop series almost all exceeded 32 per cent. Ginning outturn was only measured on one sample of *yucatanense*, but all accessions were similar in this respect, and something of the order

TABLE 4

G. hirsutum. *Central American accessions*
Node number and number of vegetative branches

Race and source	No. of accessions	Node number		Vegetative branches	
		Early sown	Late sown	Early sown	Late sown
1. *morrilli*					
Oaxaca	4	24·0	16·8	15·0	9·8
Puebla and Morelos	6	31·8	20·0	22·0	9·7
2. *richmondi*					
Salina Cruz	6	22·0	15·3	17·5	9·8
Chiapas	1	13·0	13·0	10·3	4·0
3. *palmeri*					
Guerrero	3	29·3	21·1	19·7	13·4
Chiapas	2	27·5	19·4	21·4	15·4
4. *punctatum*					
Yucatan and Campeche	13	20·5	15·7	13·9	7·8
Peten	20	20·7	14·4	13·2	8·6
Chiapas	3	12·3	11·7	10·3	6·7
6. *marie-galante*					
Guatemala and El Salvador	15	34·4	21·2	19·8	6·9
7. *latifolium*					
Central Guatemala	12	11·5	9·2	4·8	1·5
Chiapas (house yard)	13	9·8	8·2	4·9	2·2
Chiapas (field crop)	15	8·6	8·1	4·3	3·4
Coastal Guatemala	29	9·7	8·4	4·4	2·2

of 20 per cent. may be accepted as a representative figure. The low staple length of *yucatanense* may be noted. Its lint is as poor in quality as any produced in the New World, but it is quite spinnable, and is in fact, superior in length and fineness to that of some commercial Asiatic cottons of the present day. Data on lint length and ginning outturn are given in tables 5 and 6.

Boll size data are given in table 7. Except in race *richmondi*, the bolls of the perennial races rarely contain more than 2·4 gm. of seed cotton. In *richmondi* there are types with 3·0 to 4·8 gm. of seed cotton per boll. In *latifolium*, a much wider range of boll size is to be found, running in general from 1·0 to 4·5 gm. of seed cotton, except in the Chiapas field crop series. This group is remarkable for its very large bolls, with contents ranging from 4·7 to 8·4 gm. of seed cotton.

Data on seed fuzz type and lint colour are given in tables 8 and 9.

TABLE 5

G. hirsutum. *Central American accessions. Lint length*

Race and source	No. of accessions	Halo length (mm.)																	Mean
		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
1. *morrilli*																			
Oaxaca	*68*	...	...	2	1	7	4	13	8	11	5	8	5	...	4	...	...	...	25·5
Puebla and Morelos	*8*	...	...	...	...	...	...	...	...	...	...	1	3	...	1	1	1	1	30·6
2. *richmondi*																			
Salina Cruz	*8*	...	...	...	...	...	...	...	...	...	...	1	2	...	1	3	1	...	30·8
Oaxaca	*5*	...	...	...	...	...	...	1	1	1	...	1	...	1	...	...	...	...	26·6
Chiapas	*3*	...	...	...	...	...	...	...	...	...	...	1	...	1	1	...	...	...	29·7
3. *palmeri*																			
Guerrero and W. Oaxaca	*49*	...	...	1	...	...	...	3	3	13	10	9	4	2	4	...	...	...	27·1
Chiapas and Yucatan	*4*	...	...	...	...	1	...	1	...	1	1	...	...	...	...	...	...	...	24·8
4. *punctatum*																			
Yucatan and Campeche	*28*	...	...	1	...	1	4	5	6	4	6	1	...	...	...	...	...	...	24·9
Peten	*23*	...	...	...	...	...	...	...	1	1	1	3	5	5	4	2	1	...	29·3
Motagua Valley	*8*	...	...	...	...	1	1	1	1	2	1	1	...	...	...	...	...	...	25·1
Chiapas	*6*	...	...	...	...	...	...	...	...	1	3	...	1	1	...	...	...	...	27·7
5. *yucatanense*																			
Yucatan Coast	*9*	3	...	2	2	...	1	...	1	...	...	...	...	...	...	...	...	...	20·4
6. *marie-galante*																			
Guatemala and El Salvador	*28*	...	...	...	3	2	2	4	3	4	5	5	...	...	...	...	...	...	25·1
7. *latifolium*																			
Central Guatemala	*89*	1	1	1	2	2	3	8	12	15	11	12	11	4	3	3	...	...	26·5
Chiapas (house yard)	*14*	...	...	...	...	...	...	...	1	1	3	2	3	2	...	2	...	...	28·5
Chiapas (field crop)	*16*	...	...	...	...	...	...	...	...	1	1	...	1	7	4	2	...	...	30·0
Coastal Guatemala	*29*	...	...	...	1	...	...	2	3	4	4	8	2	...	3	1	...	1	27·5
Oaxaca (*morrilli* region)	*11*	...	...	...	...	1	...	1	2	1	1	1	1	3	...	...	...	...	26·9
Guerrero (*palmeri* region)	*20*	...	...	...	...	2	1	2	4	4	5	2	...	...	...	...	...	...	25·5

TABLE 6

G. hirsutum. *Central American accessions. Ginning outturn*

Race and source	No. of accessions	Ginning outturn (per cent.)																										Mean
		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
1. *morrilli*																												
Oaxaca	67	...	...	...	2	1	2	3	6	11	10	10	7	4	4	4	2	1	...	...	...	...	...	...	...	...	...	...	27·5
Puebla and Morelos	6	...	...	...	2	1	1	...	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	23·3
2. *richmondi*																												
Salina Cruz	8	...	...	...	...	...	...	1	...	3	...	2	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	27·4
Oaxaca	5	...	...	...	1	...	...	...	3	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	24·6
Chiapas	3	...	...	...	...	...	...	...	1	...	1	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	27·3
3. *palmeri*																												
Guerrero and W. Oaxaca	47	...	...	...	...	...	...	...	...	1	3	6	6	19	11	...	1	...	...	...	...	...	...	...	...	...	...	...	29·6
Chiapas and Yucatan	4	...	1	...	...	...	...	...	...	...	...	1	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	26·8
4. *punctatum*																												
Yucatan and Campeche	28	...	...	...	...	...	...	1	2	9	9	2	2	1	1	...	1	...	...	...	...	...	...	...	...	...	...	...	27·1
Peten	23	...	...	...	...	...	...	...	1	1	...	4	5	8	2	1	...	1	...	...	...	...	...	...	...	...	...	...	29·4
Motagua Valley	8	...	...	...	...	...	...	...	1	1	1	2	2	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	27·8
Chiapas	6	...	...	...	...	...	1	...	3	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	25·2
5. *yucatanense*																												
Yucatan Coast	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	18·0
6. *marie-galante*																												
Guatemala and El Salvador	22	...	...	...	...	...	...	...	...	1	2	1	1	2	2	...	2	5	5	1	...	...	...	...	...	...	...	...	32·1
7. *latifolium*																												
Central Guatemala	36	...	...	...	...	...	...	1	2	3	6	5	1	4	3	2	1	...	2	2	...	1	...	...	1	...	1	1	30·9
Chiapas (house yard)	14	...	...	...	...	...	...	...	1	1	...	1	2	4	...	1	3	...	...	...	...	...	...	1	...	...	...	...	30·6
Chiapas (field crop)	16	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	1	2	1	2	4	...	2	...	1	1	38·1
Coastal Guatemala	29	...	...	...	...	...	2	...	1	3	3	...	...	...	3	...	5	3	4	1	1	1	2	...	...	...	...	...	31·7
Oaxaca (*morrilli* region)	11	...	...	...	...	...	...	...	...	...	...	...	1	1	...	1	1	1	3	1	1	1	...	...	...	...	...	...	34·0
Guerrero (*palmeri* region)	20	...	...	...	...	...	...	...	...	...	...	...	...	...	...	3	2	6	6	...	2	1	...	...	...	...	...	...	34·4

TABLE 7

G. hirsutum. *Central American accessions. Seed cotton per boll*

Race and source	No. of accessions	Seed cotton per boll (gm.)																				Mean
		0·9 1·0	1·1 1·2	1·3 1·4	1·5 1·6	1·7 1·8	1·9 2·0	2·1 2·2	2·3 2·4	2·5 2·6	2·7 2·8	2·9 3·0	3·1 3·2	3·3 3·4	3·5 3·6	3·7 3·8	3·9 4·0	4·1 4·2	4·3 4·4	4·5 4·6	4·7 4·8	
1. *morrilli*																						
Oaxaca	*4*	...	1	1	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
Puebla and Morelos	*6*	1	...	3	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
2. *richmondi*																						
Salina Cruz	*6*	...	...	...	1	1	...	...	1	...	...	...	1	...	...	1	...	...	...	...	1	2·9
3. *palmeri*																						
Guerrero and W. Oaxaca	*3*	...	...	...	2	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·7
Chiapas	*2*	...	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
4. *punctatum*																						
Yucatan and Campeche	*9*	...	...	2	5	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·5
Peten	*17*	...	...	...	2	9	4	1	...	...	...	1	...	...	...	...	...	...	...	...	...	1·9
Chiapas	*3*	...	...	...	...	1	1	...	1	...	...	...	...	...	...	...	...	...	...	...	...	2·0
6. *marie-galante*																						
Guatemala and El Salvador	*15*	...	...	2	5	4	3	1	...	...	...	...	...	...	...	...	...	...	...	...	...	1·7
7. *latifolium*																						
Central Guatemala	*12*	...	1	...	1	2	3	2	2	...	...	...	...	1	...	...	...	...	...	...	...	2·0
Chiapas (house yard)	*13*	...	...	...	...	...	...	...	2	...	1	2	...	4	1	1	1	...	1	...	...	3·3
Coastal Guatemala	*29*	...	...	...	1	...	1	1	2	3	...	2	2	3	2	4	2	3	3	...	...	3·3
Oaxaca and Guerrero	*3*	...	...	...	...	...	...	...	1	1	...	...	...	1	...	...	...	...	...	...	...	2·8
		4·7 4·8	4·9 5·0	5·1 5·2	5·3 5·4	5·5 5·6	5·7 5·8	5·9 6·0	6·1 6·2	6·3 6·4	6·5 6·6	6·7 6·8	6·9 7·0	7·1 7·2	7·3 7·4	7·5 7·6	7·7 7·8	7·9 8·0	8·1 8·2	8·3 8·4		
7. *latifolium*																						
Chiapas (field crop)	*15*	1	...	2	1	1	...	2	1	1	...	...	1	2	...	2	...	...	...	1	...	6·3

Fuzzy seed is the commonest condition, tufted seed being rare or absent in *yucatanense*, *morrilli*, *richmondi*, *palmeri*, and *marie-galante*. Between 15 and 20 per cent. of the *latifoliums* were tufted, and about two-thirds of the *punctatums*. Fuzz colour and lint colour go together.

TABLE 8

G. hirsutum. *Central American accessions*

Fuzz type and fuzz colour

Race and source	Fuzz type				Fuzz colour				
	Fuzzy	Semi-fuzzy	Tufted	Mixed fuzzy-tufted	White	Greenish	Green	Brownish	Brown
1. *morrilli*									
Oaxaca	63	...	3	2	...	...	66	1	1
Puebla and Morelos	7	1	...	...	...	...	6	...	...
2. *richmondi*									
Salina Cruz	8	...	...	...	...	2	1	5	...
Oaxaca	5	...	...	...	...	...	5	...	...
Chiapas	4	...	...	...	...	3	...	1	...
3. *palmeri*									
Guerrero and W. Oaxaca	48	...	1	1	...	...	49	1	...
Chiapas and Yucatan	2	...	2	...	...	...	...	...	4
4. *punctatum*									
Yucatan and Campeche	12	7	8	1	14	...	1	1	12
Peten	2	2	19	...	23	...	...	...	...
Motagua Valley	...	...	8	...	8	...	...	...	...
Chiapas	6	...	...	...	...	5	...	1	...
5. *yucatanense*									
Yucatan coast	9	...	...	...	...	...	...	9	...
6. *marie-galante*									
Guatemala and El Salvador	28	...	...	...	...	...	24	3	1
7. *latifolium*									
Central Guatemala	68	...	19	2	65	11	4	8	1
Chiapas (house yard)	13	1	...	...	3	3	4	3	1
Chiapas (field crop)	16	...	...	...	11	3	2	...	...
Coastal Guatemala	26	1	3	1	28	3	...	...	...
Oaxaca (*morrilli* region)	11	...	...	...	...	1	10	...	...
Guerrero (*palmeri* region)	4	...	5	11	12	...	...	3	2

Brown lint is associated with brown fuzz, or sometimes with green fuzz. Bright white lint, which is only found on types with white fuzz, is commonest in *punctatum* and *latifolium*. Green fuzz and off-white lint are characteristic of *morrilli*, *palmeri* and *marie-galante*. Brown fuzz and brown lint are the rule in *yucatanense*.

3. NOTES ON THE RACES

(1) *Race* morrilli

Cook and Hubbard (1926) described a wild plant from the coast of Sonora, Mexico, as *G. morrilli*. Their Sonora plant is indistinguishable from a large group of perennial shrubby cottons from the central Mexican plateau in the States of Oaxaca, Morelos and Puebla.

TABLE 9

G. hirsutum. *Central American accessions*
Lint colour

Race and source	Bright	Creamy	Dull	Grey	Pale Brown	Medium Brown	Dark Brown	Rusty Brown
1. *morrilli*								
Oaxaca	1	33	10	11	...	3	3	7
Puebla and Morelos	5	...	1	...	...	...	...	...
2. *richmondi*								
Salina Cruz	2	4	1	...	...	...	...	...
Oaxaca	...	3	1	1	...	...	...	...
Chiapas	2	1	...	...	...	...	...	...
3. *palmeri*								
Guerrero and W. Oaxaca	6	41	1	...	...	1	...	...
Chiapas and Yucatan	...	...	...	...	...	2	2	...
4. *punctatum*								
Yucatan and Campeche	8	4	1	1	...	10	3	...
Peten	16	5	2	...	...	...	...	...
Motagua Valley	2	3	3	...	...	...	...	...
Chiapas	2	3	1	...	...	...	...	...
5. *yucatanense*								
Yucatan Coast	...	...	...	2	...	7	...	...
6. *marie-galante*								
Guatemala and El Salvador	...	4	2	16	6	...	...	...
7. *latifolium*								
Central Guatemala	12	7	7	...	...	1	...	...
Chiapas (house yard)	8	...	...	1	...	1	...	1
Chiapas (field crop)	10	1	2	...	1	1	...	...
Coastal Guatemala	4	10	3	...	...	...	...	...
Oaxaca (*morrilli* region)	1	4	6	...	...	...	...	...
Guerrero (*palmeri* region)	2	14	2	...	1	...	...	1

Outstanding features are their stout upright habit, and profuse development of vegetative branches. The latter soon equal or overtop the main stem, giving a rounded bush. Leaves and stems are usually densely hairy. The bolls are small and round, and do not open widely. The Puebla and Morelos types are generally taller and more

open than those from Oaxaca, and have rather longer lint and a lower ginning outturn. In other respects the race is morphologically uniform.

Seed was obtained from the United States Department of Agriculture of four of the Sonora and Sinaloa types described by Cook and Hubbard as distinct species, and living material was compared with that in the new Central American collections. Cook and Hubbard's *G. morrilli* and *G. dicladum* are within the range of the group here described as race *morrilli*. Their *G. patens* resembles *morrilli* in habit, but it is nearly glabrous. The fourth type, *G. contextum*, is nearer race *punctatum*.

The area of race *morrilli* is sharply delimited to the south. It does not occur in the extensive series from Guerrero nor is it found south of the edge of the plateau in Oaxaca, and it has not been recorded from Chiapas. Cook and Hubbard's collections provide the only information on the extent of its distribution to the north.

(2) Race richmondi

This very distinct type does not appear to be covered by any of the numerous names that have been applied to the cottons of Central America. The first, and most characteristic, material was that collected by Richmond in the region of Salina Cruz, Mexico. When well grown, *richmondi* plants are large, lax, much branched shrubs with flexible stems that tend to sprawl on the ground when carrying a crop. They are generally without much anthocyanin pigmentation, and are glabrous or only slightly hairy. The bolls are usually larger than those of *morrilli* and *palmeri*. The distribution is limited. It was the only type collected by Richmond in the region of Salina Cruz on the south coast of the Isthmus of Tehuantepec. It was also found among the highly variable cottons of the State of Chiapas (Richmond's collection), and among the dominant *morrilli* in Oaxaca as far inland as Ocotlan and Ejutla (Ware and Manning's collection). In Oaxaca and Chiapas intermediates occur between *richmondi* and other races, but in the region of Salina Cruz it is morphologically uniform. Its area is evidently small, since at Pochutla (on the south coast of Oaxaca) on the west, Ware and Manning found *latifolium* only, and on the east it does not reach the *latifolium* tract of the Guatemala coast.

(3) Race palmeri

The *palmeri* cottons all have deeply laciniated leaves, and have therefore caught the eye of plant collectors. Watt (1907) has described laciniate-leaved cottons from Central America under four specific names. All four are forms of *G. hirsutum*. Three of them (*G. palmeri*, *G. fructiculosum*, and *G. lanceolatum*) belong to this race, and the fourth (*G. schottii*) includes both this type and laciniate-leaved Uplands.

Palmeri is the name most used, and is therefore adopted. Besides their laciniate leaves the *palmeri* cottons are distinguished by their habit. They are sturdy, upright shrubs with short internodes and many ascending vegetative branches. The latter do not equal the main stem in height and a typical shrub is consequently pyramidal in outline. They are glabrous, usually with strong anthocyanin pigment in the stems and petioles, and bear a prolific crop of small, widely opening bolls. *Palmeri* is the only perennial cotton in collections from the Mexican State of Guerrero, and from the neighbouring coastal region in western Oaxaca. A collection of 49 types from this area was extremely uniform. Elsewhere it has only been found rarely (once in 10 collections in Puebla and Morelos, twice in 43 in Yucatan, and twice in 43 in Chiapas). The four Chiapas and Yucatan types have brown lint, but from the main area, brown lint was only present in one out of 49 collections. Mauer (1930), reporting on Bukasov's collections, stated that it was wild, but from field notes by Richmond and Ware and Manning, it is evident that it does not occur in natural vegetation, but in house yards, hedgerows and abandoned clearings. In field cultivation it has been replaced by *latifolium* in recent years.

(4) Race punctatum

G. punctatum Sch. et Thon., *G. hirsutum* var. *punctatum* J. B. H. This is the best known of the perennial races of *G. hirsutum*. It was originally described from West Africa, where it has been established since the end of the eighteenth century (Hutchinson, 1949). The *punctatums* are slender-stemmed shrubs with a number of spreading vegetative branches. Under favourable conditions they crop heavily, and the slender main stem becomes decumbent, while the spreading vegetative branches lie prostrate on the ground. Anthocyanin pigment is generally well developed. Stems and leaves are glabrous or nearly so. The leaves are characteristic, being usually very shallowly cut into three obtuse lobes, the lateral lobes ascending so that the leaves have a parallel-sided appearance. Bolls are medium to small, the lint is short and the ginning outturn low, so that in spite of prolific bolling, the crop is not large and is expensive to pick and gin. Hence, in spite of a wide adaptability, the race is of little use as a commercial cotton.

In Central America, *punctatum* is extremely common in Yucatan, where it is very variable, in the Peten region of Guatemala, where Stephens reports that the whole process of establishment of house yard types in the wild can be seen, and in neighbouring British Honduras. An early fruiting form occurs in Chiapas, and intermediates are there to be found between *punctatum*, *richmondi* and *latifolium*. The typical form occurs round the coasts of the Gulf of Mexico to Florida and the Bahamas. It was the first cotton to be cultivated in what is now the United States of America (Hopi and Moqui Indian

cotton). In the Greater Antilles a xerophytic form is to be found wild in scrubby vegetation on the dry leeward sides of some of the larger islands.

Punctatum has been widely distributed in the Old World (see Hutchinson, 1947). It has been very successful in house yards and small cultivations throughout the West African and Sudan savannah regions from the Gambia and Senegal to the Red Sea. Here, further differentiation has taken place. In West Africa an early annual form has been developed which is grown in small field plots, and in Egypt, a specialised type has become established as a weed in crops of the more valuable Egyptian cotton. In response to the requirements of this habitat the " Hindi weed," as it is called, has developed the quick germinating, rapid growing, and early fruiting characteristics necessary for survival in an annual crop.

Punctatum has played a most important part in the development of resistance to blackarm disease in New World cottons acclimatised in Asia and Africa. Knight and Hutchinson (1950) have shown that one or more genes for resistance to blackarm disease occur commonly in *punctatum* in the Bahamas, and there can be little doubt that the existence of blackarm resistance in the introduced stock has contributed greatly to its widespread success in the Old World. In West Africa, among both annuals and perennials, lines are to be found with varying degrees of resistance up to virtual immunity, and resistance has been found in types acclimatised in India and northern Australia. Moreover, where *latifolium* has been introduced in the Old World, it has almost always been preceded or accompanied by *punctatum*, and Knight and Hutchinson (1950) have shown that the blackarm resistance now commonly to be found in the acclimatised forms of *latifolium* can be traced to hybridisation with *punctatum*.

(5) *Race* yucatanense

This race has not previously been described. It was collected by Stephens, who reported that it was growing wild in natural vegetation on coastal sand dunes in the region of Progreso, Yucatan. The sand dune region is cut off from the mainland by a swampy tract, so these cottons probably enjoy a fair degree of isolation. The plants are small, much branched, procumbent or prostrate, and glabrous or nearly so. Anthocyanin pigmentation is usually slight, The leaves resemble those of *punctatum* in being very shallowly divided into ascending lobes, giving a parallel-sided appearance. The bolls are small and open widely. The lint is brown, short and scanty, and the seeds have hard seed coats and delayed germination. Variability is low.*

* Dr Stephens comments: " In respect of habit, no doubt, but the population I collected was segregating for simple mendelian genes, anthocyanin, corolla colour, lint colour, hairiness. Presumably the uniformity only applies to characters of high selective value."

Punctatum has given rise in many parts of its range to forms which have become established in natural vegetation. *Yucatanense*, which is obviously closely related to *punctatum*, is the most extreme of these, having developed the specialised procumbent habit, but " algodon brujo " of Cabo Rojo in Puerto Rico (Hutchinson, 1944), " *G. ekmanianum* " of Haiti, and " *G. taitense* " of the Polynesian Islands all resemble it in their small bolls, poor and scanty lint, and small hard seeds. This last is a characteristic of the truly wild species of *Gossypium*, and since it spreads germination over more than one season, it has obvious advantages for a wild plant in a xerophytic environment.

(6) Race marie-galante

G. hirsutum var. *marie-galante* J. B. H. This race includes the largest and most tree-like of all the cottons. The Guatemalan and Salvadorean types, however, are shrubby,* and no larger than the other Central American races, to which they are evidently closely related. The *marie-galantes* are highly photoperiodic, much branched shrubs. One of the chief characteristics of the race is the dominance of the main stem, and in the large West Indian and Brazilian types this results in the development of a small tree with a trunk that may be 5 or 6 inches in diameter. This is in strong contrast to *morrilli*, *richmondi* and *punctatum* in which the lateral branches soon equal or exceed the main stem, and an old plant develops into a bushy thicket and not a tree.

The Central American types have small bolls and small seeds, with short but copious, usually greyish, lint. In the Stephens and Ware-Manning collections there were two rather distinct types, one glabrous with strong anthocyanin pigmentation, and the other bearing a coat of short hair, and having little anthocyanin pigment.

Marie-galante was originally described from the West Indies. It was first recorded from Central America by R. A. Silow (personal communication), who noted that two specimens from the Pacific Coast of Costa Rica in the Gray Herbarium might well belong to this race. From his description they appear to be similar to those collected by Stephens in coastal Guatemala and El Salvador. Stephens obtained a considerable series, and Ware and Manning added to it, but the race seems to be confined to the Pacific slopes from Escuintla eastwards. There is every reason to believe that the distribution is continuous from Guatemala to Colombia, where larger, better quality forms provide the commercial crop of the Atlantico Province. The race is common throughout the Caribbean region and in north Brazil, and on the west coast of South America it extends southwards from

* Dr Stephens comments : " This is not completely true. I did find tree types 15 ft. high or more but they were not bolling when I collected. I remember 3 of the finest specimens I have seen in a garden in Santa Lucia, Guatemala. These were larger and taller than any I have seen in the West Indies. However, on the whole, the *marie-galantes* were small and shrub-like but with a pronounced main stem."

Colombia to Ecuador. It has undergone considerable differentiation in response to the demands of perennial cultivation. The cultivated forms are large and tree-like, and include a great range of types in respect of such characters as plant hairiness, boll size, seed type, staple length, and lint quantity. Moreover, in the open vegetation of xerophytic habitats on the coasts and islands of the Caribbean, it has become established in the wild, and there are now to be found types with the scanty lint, hard seed coats, and delayed germination that characterise the wild cottons of many races.

Further differentiation has occurred following hybridisation. In the North Brazilian States of Rio Grande de Norte and Ceara, Harland (1939) reported that the introduction of Upland (*latifolium*) has resulted in the development in the commercial crop of a hybrid stock almost to the exclusion of pure *marie-galante*. On the Gold Coast, where the race is well established in house yards in the southern forest region, spread into the northern savannahs has been made possible by the acquisition of blackarm resistance by introgressive hybridisation with *punctatum* (Hutchinson, 1949).

(7) *Race* latifolium

From *G. latifolium* Murray (see Watt, 1907). Sub-shrubs growing as annuals in field crops, or persisting for a few years as house yard plants. These include the most advanced products of man's selection as crop plants. Many of the Central American forms have enough photoperiodic response to prevent satisfactory fruiting in more northern latitudes (Ware, 1936), but types capable of crop production in long days have been selected and have given rise to the commercial cottons of the American Cotton Belt, commonly known as Uplands, and thence to crops in many other parts of the world. *Latifolium* includes a great range of types with medium large to very large bolls, and copious lint of fair to good quality.

The centre of the race is in central and northern Guatemala and the neighbouring State of Chiapas in Mexico. It is now established as a commercial crop on the south coast of Guatemala, where it was collected by Richmond and Stephens. Ware and Manning found it in small field crops in Oaxaca and Guerrero also, but were informed that it had been introduced there within living memory.

The Guatemalan collections are highly variable in plant habit, hairiness, anthocyanin pigmentation, boll size, productivity and other characters. In Chiapas the Guatemalan type is to be found in house yards, differing little from that of central Guatemala except in the frequency of larger bolls. In small field crops, on the other hand, a very distinct form is grown. This is a rather lax and sprawling, glabrous plant, with large leaves. It has very large bolls, outside the range of all other Central American forms of the species. Moreover, it is uniformly high in ginning outturn, and is one of the few Central

American groups to reach a mean lint length of 30 mm. It is of considerable agricultural importance, as types collected in the vicinity of Acala in Chiapas gave rise to the Acala variety and its derivatives in the United States Cotton Belt.

Further west in the *morrilli* and *palmeri* areas *latifolium* is generally to be found in small field plots, whereas the perennial races are house yard cottons. In both areas the influence of the old-established perennial on the immigrant *latifolium* is very evident. In Oaxaca the Uplands have developed, doubtless following hybridisation with *morrilli*, the characteristic upright habit and ascending vegetative branches of the latter, and the dense coat of long hairs on both upper and lower surfaces of the leaves. In Guerrero, the laciniated leaf of *palmeri* has not been transferred, doubtless because it forms such a ready index of contamination and would therefore be eliminated. The transfer of *palmeri* genes is evident, however, in the strong stem and petiole pigmentation and the comparatively glabrous stem tips and leaves of Guerrero accessions. In both areas some differentiation in seed cotton and lint characters is evident. Ginning outturn is high, and boll size is above that of the central Guatemalan type. In the *morrilli* region all accessions had the green fuzz characteristic of *morrilli* itself, whereas in Guerrero the white fuzz more usual in *latifolium* predominated, though *palmeri* has green fuzz.

Latifolium has spread over vast areas in post-Columbian times, having been carried to the United States Cotton Belt, where it gave rise to the Upland cottons, and to most of the cotton-growing countries of the world. The race was established in Carolina at the beginning of the eighteenth century (Watt, 1907), but did not become a major crop until the ginning problem was solved by the invention of the saw gin by Whitney in 1793. Thereafter the American Upland crop rapidly achieved a dominant place in the world's cotton markets, and other cotton-growing countries, both actual and potential, began introducing Upland seed. The development of the crop, first in America and later in India and Africa, has been discussed elsewhere (Ware, 1936 ; Hutchinson, 1938 and 1947 ; Hutchinson and Silow, 1947 ; Knight and Hutchinson, 1949). Suffice it to say that acclimatisation in the United States Cotton Belt involved selection for long day fruiting and early and prolific cropping, and was accompanied by the development of high quality in some lines. Success in India and Africa, on the other hand, depended primarily on the spread of genes for resistance to the jassid pest and blackarm disease.

Though most of the acclimatised *latifolium* stocks of the Old World are derived from the Uplands of the United States Cotton Belt, the important south Indian Cambodia can be traced by way of Cambodia and other parts of southeast Asia (Main, 1912) to direct introductions by the Spaniards from Mexico to the Philippines (Lewton, 1925). In India the Uplands and Cambodias have developed side by side. The Uplands are descended from introductions by the East India

Company in the middle of the nineteenth century. Though initially a failure as a crop, they became established in the Dharwar district of the Deccan, and after a period of natural selection for resistance to jassid and blackarm (see Hutchinson, 1938 and Knight and Hutchinson, 1950), they gave rise to the modern Indian American crops of the Punjab and Sind, and to a less extent of Central India and the northern Deccan. The Cambodias were a late introduction, but had been subject to selection in south-east Asia for a long period, and had developed the highest level of jassid resistance known in the race. Following their success in the Madras Presidency they were widely distributed in more northerly regions. Never having been through the United States Cotton Belt they have not been selected for long day fruiting, and it is probably for this reason that they have failed to compete with the Uplands in northern India.

The distribution of these two *latifolium* stocks is of considerable importance to the plant breeder. When grown together they can be readily distinguished. In an Indian collection grown at Namulonge in 1949-50 the Uplands produced few vegetative branches of little value to the crop, and grew into slender plants with rather small leaves and bolls. The Cambodias produced several stout vegetative branches per plant which contributed considerably to the crop and developed into bushy plants with stout stems, large fleshy leaves and rather large bolls. The sources of accessions of the two types were distributed as follows :—

Locality	Cambodia	Near Cambodia	Near Upland	Upland
Coimbatore (Madras) . . .	5	...	...	...
Dharwar and Parbhani (Deccan) .	...	1	2	3
Central India	...	3	1	2
United Provinces and the Punjab .	...	...	...	8
Chitral	...	...	...	2

It will be seen that material from the two Deccan stations was predominantly of the Upland type, as might have been expected from the fact that it was at Dharwar in the Deccan that the Upland cottons were first established. In Central India, Coventry distributed a considerable quantity of Cambodia in an area in which Upland was already present as a mixture in the indigenous *arboreum* crop (Hutchinson and Ghose, 1937). In consequence, the two types are now about equally frequent, though the Cambodias show signs, in their rather finer wood and smaller leaves, of gene exchange with the Uplands. Further north, in the Indo-Gangetic plain and in the Himalayan valleys, all the *latifolium* cottons are of the Upland type.

In other parts of Asia, the Cambodia type is only known from Indo-China and the Philippines. A *latifolium* collection from south China and Formosa was more like the Uplands than the Cambodias,

and is probably entirely of Upland origin. Russian Uplands appear to be closely related to those of the American Cotton Belt to-day, and those of Persia are similar.

The *latifolium* cottons of Africa are more recent introductions than those of India, little having been done on the crop until the first decade of the present century. They are all Uplands, the early introductions having been of long stapled crop varieties from the American Cotton Belt. The major selective factors in Africa have been similar to those in India. Jassid is a major pest and blackarm a serious disease in most of the rain-fed cotton tracts except the Belgian Congo, and present-day African Uplands contain a high proportion of hairy (jassid-resistant) plants and of plants carrying at least one major gene for blackarm resistance (see Knight and Hutchinson, 1950). In the Congo, on the other hand, where jassid and blackarm are not serious, modern American crop varieties are successfully grown.

The selection pressures exercised by jassid and blackarm have resulted in the development of a type more like the Uplands of northern India than those of the United States. Many points of difference exist, however. The African Uplands were derived from the best quality American varieties of the time, and a higher standard of quality has been maintained than is found in the Indian Uplands and Cambodias. In the East African cottons a tall, leggy type with short fruiting branches is common. It is a slow and rather mediocre cropper, but has the virtue of recovering well from attacks of blackarm and bollworm that would cripple a quick cropping strain. Such a form would never survive in the short season of the Indian cotton tracts. On the other hand, as a result of the breeding work carried on at Barberton in the Eastern Transvaal, a quick cropping, very prolific type (U4) has been isolated and spread in the Transvaal, Portuguese East Africa and Nyasaland.

It will be seen that in race *latifolium*, establishment in the Old World has resulted in the development of highly variable stocks. Rapid communications have made for easy seed exchange, and even types of such widely different histories as the Uplands and Cambodias have not been grown in isolation long enough to have developed such distinctive characteristics as separate the races in Central America. Moreover, differentiation in response to such powerful selective forces as the jassid pest and blackarm disease is as yet in its early stages, susceptible types still being common in all but pedigree stocks from breeding stations.

4. DISCUSSION

The primary object of the Central American expeditions was the collection of material of value for cotton breeding projects. Following Vavilov (1935), it was believed that in the region of origin of a crop plant the variability is at a maximum, and genes are present that are

rare or absent from the more recently colonised peripheral areas. From the plant breeder's point of view, the collections have proved somewhat disappointing. Considering the species as a whole, a great range of variability exists in a small area, but a large part of it is assorted between well-defined races, and being largely a matter of diversity in the perennial habit, is of little interest to the breeder of annual cottons. Moreover, even where the intra-racial variability is large—in the perennial race *punctatum* and the annual *latifolium*—almost the whole Central American range in characters of agricultural value lies below that to be found in modern commercial crops and the gene content in respect of resistance to pests and diseases is inferior to that of the acclimatised forms of the Old World. For an understanding of the development of the species, on the other hand, the collections are of the greatest value, since the discovery of the partition of the greater part of the variability between distinct and often very uniform races indicates a more advanced evolutionary status than was anticipated.

Wild forms, which have often been regarded as primitive, are known in four of the seven races of *G. hirsutum*. *Yucatanense* only exists as a wild plant. Wild forms of *punctatum* are to be found in xerophytic scrub on coastal sands in Puerto Rico, in dry areas in Haiti, on the Florida Cays, on numerous islands of the Pacific, and in northern Australia. In *marie-galante*, wild types are known from xerophytic scrub in Jamaica, St Kitts, Nevis, Antigua, Barbados and coastal Colombia. The original type of *morrilli* was collected in the wild on coastal sands in Sonora, Mexico. These forms, wherever they are found, have certain characters in common. They are slow growing, long lived perennials, and they have small bolls and small seeds with hard seed coats and inferior, scanty, and firmly attached, lint. Though they have been regarded as primitive, a little consideration will show that the characters they have in common are at least as readily explained as the consequence of convergent evolution as of common ancestry. This complex of characters is common to all wild species of *Gossypium*, and to the wild forms of the Asiatic cottons and of *G. barbadense*, as well as to those of *G. hirsutum*. All save the inferior and scanty lint are obviously advantageous in the xerophytic scrub vegetation in which wild cottons are found, and scanty lint firmly attached to the seed may well be associated with a hard seed coat.

It should be emphasised that the lint of all wild forms of *G. hirsutum*, though inferior in quality to that of the cultivated forms, is nevertheless spinnable and is in fact superior to that of some current commercial Asiatic cottons. There is therefore no force in the argument that the wild cottons must be primitive because their lint can never have been used.

All the wild forms of *G. hirsutum* listed above are to be found in peripheral areas. On the three Central American collecting expeditions

a search was made for truly wild populations growing in natural vegetation. Richmond and Ware and Manning reported, however, that the whole of their collections came from field crops, house yards, hedgerows, and similar man-made habitats.*

Stephens reported that except in two localities, cotton was only to be found in, or close to, villages, in places where it had either been deliberately planted, or to some extent tended directly or in the course of cultivation of more important crops. The two exceptions were on the coastal sands of Yucatan, where *yucatanense* is fully established in the wild, and in the Peten region of northern Guatemala. There he found *punctatum* in all stages of the process of escape from cultivation. At one extreme were house yard cottons receiving a certain amount of care and protection, and at the other were plants fully established in natural vegetation. When grown in culture in the Sudan, those descended from wild plants were indistinguishable from the house yard cottons, and the whole series evidently belonged to the house yard *punctatums* that are widely spread throughout the Yucatan peninsula. No other example of a truly wild cotton was found, and it may therefore be accepted that in eastern Mexico and Guatemala, *G. hirsutum* is entirely a domestic or commensal plant.

It might be argued that the wild prototypes have been supplanted by their cultivated derivatives at the centre of cultivation, and those now found in peripheral areas are the relics of a formerly widespread race. Wild cottons, however, only grow in xerophytic habitats with open vegetation (Hutchinson, 1944) and where cultivated and wild forms are found in neighbouring areas they do not compete with each other, since the habitat of the wild form is unsuitable for cultivation. Hence there is no reason to suppose that a wild prototype of *G. hirsutum* would be extinguished by its derivatives cultivated in more mesophytic situations.

There is thus good evidence from their distribution alone for ignoring the wild forms in the search for the prototype of *G. hirsutum*. The morphological evidence against them is even stronger. The wild forms do not form a homogeneous group, as would be expected in relics of a former widespread race, but bear all the characteristics of the cultivated races of the areas in which they occur. The small house yard forms of *marie-galante* from Guatemala and El Salvador are not very different from the *punctatums* of neighbouring areas. The more tree-like forms that are to be found wild in the Lesser Antilles, on the other hand, are generally similar to the cultivated *marie-galantes* of the same region. They are widely different from the wild *punctatums* of the Greater Antilles, which in turn resemble the cultivated and commensal forms of their own race that are to be found in fields and

* Wild lintless diploid species of *Gossypium* are, of course, indigenous in Mexico, and one of them, *G. gossypioides*, was collected by Richmond and also by Ware and Manning, in natural xerophytic scrub on the Pan-American highway 60-80 m. south of Oaxaca City.

house yards nearby. Similarly, *yucatanense* is obviously related to the variable commensal *punctatums* of Yucatan, rather than to the wild forms of other races, and the wild *morrilli* of Sonora can be matched by cultivated forms of the same race from further south, and not by wild forms from other parts of the Americas. Evidently the development of the wild forms was subsequent to the differentiation of the races, and their possession of a group of characters in common must be the consequence of convergent evolution under the selection pressure of similar ecological situations.

Since the wild forms of *G. hirsutum* throw no light on the differentiation of the species, the problem may be approached from a consideration of the relationships between *G. hirsutum* and its nearest relative. *G. hirsutum* is sufficiently close to *G. barbadense* to give a fully fertile hybrid in F_1, though distinct enough to cause extensive genetic breakdown in F_2 and later generations. Since it has been shown above that the most important inter-racial differentiation in *G. hirsutum* is in habit characters, it is reasonable to regard as primitive those forms of the species that are closest to *G. barbadense* in growth form. Habit differentiation in *G. barbadense* is small compared with that in *G. hirsutum*, and all types, even the wild var. *darwinii*, are rather tall, upright shrubs in which the main stem retains its dominance over the lateral branches. This is the form characteristic of the Central American types of race *marie-galante*, and accepting it as primitive, a consistent pattern of differentiation becomes apparent. Within race *marie-galante*, the size and dominance of the main stem has been intensified, giving rise to the large tree-like forms of the Caribbean region. The dominance of the main stem persists in *palmeri*, which has been differentiated by the shortening of the internodes and the establishment of the laciniate leaf. In *richmondi*, *morrilli* and *punctatum*, lateral development has proceeded at the expense of the main stem. In *richmondi* and *punctatum* the stems are flexible, and the plants tend to sprawl under the weight of the crop, whereas in *morrilli* they are stiff and upright. In *latifolium*, early fruiting has been developed, accompanied by a reduction in lateral growth which reaches the limit in some of the early Upland types, in which vegetative growth is confined to the main stem.

Viewed in this way, the position of *yucatanense* is clear. With its small size, prolific lateral growth, and prostrate habit, it is the farthest removed from the *barbadense* type of plant, and fits naturally into the sequence as a specialised derivative of *punctatum*, adapted to an exacting ecological situation.

The conclusions that cultivated forms of *G. hirsutum* are primitive, and that the present races arose by differentiation in cultivation, have important consequences for the ethnologist. Such sharp distinctions could only have been developed in isolation, and it follows that each of the six cultivated races must have arisen in the fields and gardens of an isolated agricultural community. It should therefore be possible

to match the six centres of the cultivated races mapped in fig. 1 with six corresponding foci of civilisation.

As has been noted above, the inter-racial variability is for the most part a matter of differentiation in habit characters that are of little or no value to the breeder of modern annual commercial cottons. From the point of view of the future prospects of the species as a crop plant, it is the intra-racial variability that is important, and particularly that within race *latifolium*. This will now be considered.

In intra-racial variability there is a close relationship between diversity and evolutionary success as measured by population size and recent increases in area occupied. Compare for example *palmeri*, which is one of the primary races, and *yucatanense*, which it is suggested is a secondary derivative of *punctatum*, with *punctatum* and *latifolium*. The two former are small in numbers and occupy strictly limited areas, and are very uniform. The two latter are large in numbers and have spread widely in very recent times, and they are extremely diverse throughout their range. The contrast is parallel to that demonstrated by Hutchinson and Stephens (1947) between the wild lintless species of *Gossypium*, with their small populations, relic status, and low variability, and the cultivated linted species, with large populations, wide distribution, and great diversity. The comparison may be taken further. In a survey of the native cottons of Puerto Rico (Hutchinson, 1944) two forms of *punctatum* were found. The typical house yard form was highly variable, whereas the wild "*algodon brujo*," adapted to the specialised ecological conditions of two small, dry coastal areas, was much more uniform. Diversity, in fact, is associated with evolutionary success at all levels of differentiation from the ecotype to the sub-genus.

Evolutionary success implies the achievement of a favourable balance with the selective forces of the environment. A species cannot multiply and spread unless, either on account of the emergence of a specially well fitted genotype or because of the existence of a particularly favourable environment, selective elimination is low enough to allow an increase in numbers. Under such circumstances an increase in variability may be expected (Fisher, 1930). In fact it is success, and the relatively mild impact of selection that success implies, which permits the development of variability. The effects of success are cumulative, since increasing variability means increasing possibilities of adaptive response, and hence of greater success. Moreover, under the low selection pressures that exist under conditions of success, elimination will continue low, and variability will be maintained or increased. This is the situation characteristic of the cultivated cottons. In the newly colonised areas new genotypes of high adaptive value are to be found, but selective elimination has been moderate, the new material has not excluded the old, and variability is consequently high.

These are the conditions to be found where success has been

recent and rapid, and are typical of the circumstances of modern crop plants. They do not represent the conditions when the expanding population fills the available habitats, and a new stable state is established. The achievement of stability comes about by an increase in the pressure of selection until elimination matches population increase, and during this phase a reduction in variability may be expected. The best adapted genotypes will survive to the exclusion of less fit material, and the diversity that remains will be assorted between geographical races, or along clines in a continuous population (see examples of old established, wide-ranging species cited by Mayr, 1949). The extreme case is that provided by the development of a highly adapted, uniform race fitted to survive under special and exacting conditions. Examples in *G. hirsutum* are race *yucatanense* in Yucantan and "*algodon brujo*" in Puerto Rico. These, which may be regarded as relics in the making, are the products of rigorous selection in a difficult environment and not, as Stebbins (1949) has suggested, types which "have survived largely in places where competition has been relatively little, and selection not very rigid."

The spread of *G. hirsutum* in the last few centuries is a good example of development under conditions favouring diversification. Fortunately it is so recent and has been studied so intensively, that it is possible to discuss the development of the variability now present in the newly colonised areas in some detail. The processes involved may be illustrated by a consideration of recent changes in habit characters, disease and pest resistance, and lint quality.

Habit changes have gone on in two directions. In *marie-galante*, under the circumstances of perennial cultivation large and tree-like forms have been developed. In *punctatum* on the other hand, though the Central American perennial shrubby habit is the common form throughout the range of the race, annual forms have been developed to meet the special conditions of field crop culture in the French Sudan, and of persistence as a weed ("Hindi" cotton) in the annual *G. barbadense* crops of Egypt and the Sudan. The whole range of habit is to be found in the same area in both instances, the longer lived, shrubby forms predominating where perennial growth is possible, and the early types where the annual habit is enforced. Among "Hindi" types collected from the Egyptian crop of the Sudan, for instance, a wide range of habit is to be found, from something very close to the shrubby house yard types of the rain fed regions of the country to early cropping forms that match the typical "Hindi" weed of Egyptian literature.

In *latifolium*, the potentialities of annual cropping were present in the Central American stock, though most of the types in the new collections are quite capable of persisting for several years. Truly annual forms are represented, however, by the big bolled form from Chiapas. In respect of habit it is probable that present-day collections are not truly representative of the stock of the race. Before the days

of machine-made textiles, the demand for locally grown cotton for hand weaving must have been large, and the amount of cotton grown in field crops considerable. It is a fair presumption that the earlier fruiting types suited to such conditions would be more abundant than the long-lived house yard and hedgerow forms that predominate in recent collections. The establishment of the Upland crop in the United States, therefore, involved little but the selection of the early long day forms among those already available in Central America. Subsequent changes in habit have involved little more than the continuation of this early trend. In the development of habit characters, therefore, *marie-galante* and *latifolium* may be contrasted with *punctatum*. In the two former recent developments are the natural continuation of earlier trends, whereas in the latter, the emergence of annual types in the newly colonised areas in Africa is a departure from the general line of development of the race.

Differentiation to meet the conditions of new areas has been very important in the field of disease and pest resistance. The development of blackarm resistance in New World cottons acclimatised in the Old World has been traced by Knight and Hutchinson (1950). The basis of all effective resistance was shown to be the gene B_2, which occurs rarely in *punctatum* in the New World. In the Old World it has spread in *punctatum* and has been transferred by hybridisation to *latifolium*, and there spread under the selective pressure of the disease. Moreover, it has been reinforced until a high degree of resistance is attained, on the one hand by the spread of other major genes in the *punctatums* and *latifoliums* of West Africa, and on the other by minor gene accumulation in the *latifoliums* of India.

A similar situation has arisen in respect of the hairiness that imparts jassid resistance (Parnell *et al.*, 1949). Knight (in press) has shown that resistance depends on a major gene reinforced by minor genes. In the New World major genes for hairiness are commoner than major genes for blackarm resistance, but hairiness adequate for real resistance is confined to race *morrilli*, which does not appear to have contributed to the acclimatised cottons of the Old World. The development of resistance by the synthesis of a gene complex consisting of a major gene and a group of minor genes has gone on in the Old World, probably largely independently in south-east Asia, India and Africa, and has reached its greatest development in the virtually jassid immune Cambodias.

High lint quality in *G. hirsutum* may be traced to the high quality stock of *G. barbadense* that gave rise first to the Sea Island, and later to the Egyptian cottons. The distribution of this stock has been traced by Hutchinson and Manning (1945), who showed that long and fairly fine lint is to be found among the primitive variable *G. barbadense* cottons of western South America, and suggested that the Sea Island cottons were selected in a *G. barbadense* stock brought from western South America to the Greater Antilles by the Spaniards, and thence

carried by British colonists to the Sea Islands of South Carolina. The high quality of the modern Egyptian cottons is attributable to the contribution of the Sea Islands to their ancestry (see Hutchinson, 1949). In *G. hirsutum* long lint is to be found in both *marie-galante* and *latifolium*. In *marie-galante* there are long staple types in coastal Columbia, which is on the postulated line of spread of long staple *G. barbadense* from western South America. In the West Indies, the long linted form of *marie-galante* has been identified by Hutchinson and Stephens (1944) with the " French," or " small seeded " cotton of the 18th century, and its source traced to Hispaniola, again on the supposed track of the fine linted *barbadense* cottons. High quality in *latifolium* was developed in a number of lines in the south-eastern United States, where the distribution of Upland and Sea Island overlapped. Some long staple Uplands, *e.g.* Meade, are known to have been derived from Sea Island crosses, and it may be suggested that long staple in all New World cottons is founded on genes derived from the long staple *barbadenses* of western South America.

These examples have been taken to illustrate a process that can be observed in many characters. The great range of variability now to be found in characters of importance in newly colonised areas has arisen by the spread in the population of genes that were formerly very rare. In most cases the source can be traced back to the New World, but in some instances, notably blackarm resistance in West African stocks, there seems reason to believe that the variability has been augmented by gene mutation in the new areas.

Though new gene complexes have arisen under selection, it may be concluded that selection pressure has remained relatively low, since the ancestral characters still persist in all but the most carefully bred populations. Fully blackarm susceptible plants are to be found alongside immunes and high level resistants, jassid susceptibles are common in all but the plant breeder's pedigree stocks, and the range of variation in staple length is an ever-present problem in cotton marketing.

The outstanding feature of recent diversification in *G. hirsutum* is, in fact, the synthesis of new characters in areas where they have a high selective value, on a basis of genes that were formerly very rare in the species. This implies free gene exchange through large parts of the expanding population, and has resulted, contrary to expectation on the Vavilov theory, in the development of high variability in peripheral areas. The key to the distribution of variability in crop plants is, in fact, the rate of gene exchange. Given free gene exchange, the assortment of the available variability into races or clines adapted to local conditions proceeds unhindered. Where gene exchange is limited by self fertilisation, or by excessive fragmentation of the expanding population, the development of new adaptive genotypes by recombination will be retarded. Selective elimination will go on in the existing range, however, and the nett result will be

a reduction in variability. Hence the Vavilov condition, of diminishing variability from centre to periphery, will arise where spread outruns gene exchange. In cotton, with considerable natural cross pollination and in many areas repeated introductions of material of more than one race, conditions for gene exchange have been particularly favourable, and there is no evidence of diminishing variability in peripheral areas. In an almost universally self-pollinated crop like wheat, on the other hand, it is easy to see that the speed with which man has spread the crop in recent times has been too great to allow of free assortment of the gene content of the species.

Evidently the pollination system in a crop plant has far-reaching effects on its evolutionary prospects, and merits close consideration. Rick (1950) has demonstrated that the tomato, which is self-pollinated in the recently colonised parts of its distribution, is naturally cross-pollinated in its original home, and has given evidence to show that self-pollination arose in response to selection for fruitfulness in the absence of natural pollinating agents. He thus raises the whole question of the history of self-pollination in crop plants, for where self-pollination was imposed following spread into areas where conditions were unfavourable for cross pollination, the Vavilov type of distribution of variability would naturally arise.

These considerations have an important bearing on plant breeding policy, particularly in new areas such as Africa. It is clear that an understanding of the structure and distribution of variability in a crop plant is of great value in the planning of an efficient breeding scheme. A comprehensive survey of variability makes it possible on the one hand to indicate the best sources of material for particular purposes, and on the other, to decide on the most likely areas in which to search for genes to meet new needs. For example, in the *latifoliums*, West African material is of outstanding importance for blackarm resistance, the hairiness that gives resistance to jassids is best developed in the Cambodia group (Philippines and South India), and high quality should be sought in stocks that have been in contact with the Sea Island-Egyptian group of *G. barbadense*. In more general terms, in breeding for the cotton areas of Asia and Africa, disease and pest resistance and local adaptation giving high cropping capacity are more likely to be found among the acclimatised *latifoliums* of the Old World than in fresh collections from the original area of the species.

For plant breeders concerned with the development of efficient strains in areas to which a crop plant has recently been introduced, the demonstration of the importance of high variability and free gene exchange is very significant. In their analysis of the history of blackarm resistance in New World cottons, Knight and Hutchinson (1950) have shown that if the precautions now considered necessary to safeguard the purity of breeding stocks had been taken by those responsible for the early introductions into the Old World, blackarm

resistant Uplands would never have arisen. Random interbreeding is too uncertain a system for use in breeding plots, and considerable progress has been made in substituting planned hybridisation for natural crossing in respect of those characters that have been identified and studied.* In general, however, the plant breeder works with stocks of very limited diversity, and the possibilities inherent in highly variable material have scarcely been explored.

In conclusion, the evolutionary prospects of the races of *G. hirsutum* may be assessed. *Yucatanense* has settled down to relic status already. *Palmeri*, *richmondi* and *morrilli* are little short of it. *Marie-galante* achieved some success on the Spanish Main and in Brazil but has passed its peak, and will probably develop little further. *Punctatum* has been very successful in West Africa, and will probably hold its place on the southern border of the Sahara. In range, population size, and variability, however, race *latifolium* outstrips the whole of the rest of the species, and in it most of the future evolutionary development of the species will proceed.

5. SUMMARY

Extensive new collections from the original area of *G. hirsutum* in Central America have made possible a fresh assessment of differentiation within the species. It is shown that an advanced stage of development has been reached, and that the species can be divided into seven morphologically and geographically distinct races. The greater part of the variability in the Central American material is assorted between races, and in four of the seven, intra-racial variability is low. Six of the seven races—*morrilli*, *richmondi*, *palmeri*, *punctatum*, *yucatanense* and *marie-galante*—are perennials, and one—*latifolium*—is in general annual. Only three races—*punctatum*, *marie-galante* and *latifolium*—extend beyond Central America, and the distributions of all seven are consistent with the view that they arose in Central America, and were originally allopatric.

The spread of the three more widely distributed races is discussed, and it is shown that intra-racial variability is closely related to evolutionary success as judged by population size and recent extensions in range. This relationship holds throughout the genus *Gossypium* from the sub-genus down to the ecotype. Evolutionary success is interpreted as the achievement of so favourable a balance with the environment that selection pressures are moderate. Variability will depend on selection pressure on the one hand, and on the rate of gene exchange on the other. The lower the selection pressure, the less the reduction in variability by selective elimination, and the greater the rate of gene exchange, the greater the opportunity for the synthesis of new and valuable genotypes.

* As for example, in Knight's (1946) systematic work in the transfer of genes for blackarm resistance to commercial Egyptian cottons.

The distribution of variability in the widespread races of *G. hirsutum* is discussed, and illustrations are given of the development of diversity in peripheral areas by the synthesis of new characters on the basis of genes that were formerly rare. It is shown that only under conditions of free gene exchange, such as exist in the cottons, could such high variability be maintained throughout the population. This state of affairs is contrasted with that in self-fertilised crop plants, in which it is shown that distribution by man must have outrun gene exchange, and thus inevitably led to the decay of variability in peripheral areas observed by Vavilov. Reference is made to Rick's demonstration of the change from cross- to self-pollination by the tomato when it was introduced into Europe, and it is pointed out that this alone would lead to the Vavilov type of distribution in newly colonised areas.

Knowledge of population structure and the distribution of variability is of great value to the plant breeder. Examples are given, with special reference to cotton breeding in Africa, of the value of knowledge of the distribution of variability in race *latifolium*, and attention is drawn to the importance of such knowledge for the proper planning of plant breeding policy.

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SPECIES CROSSES IN *ANTIRRHINUM*

II. CLEISTOGAMY IN THE DERIVATIVES OF *A. MAJUS* × *A. GLUTINOSUM*

K. MATHER and A. VINES
Department of Genetics, University of Birmingham

Received 15.xi.50

I. THE ORIGIN OF CLEISTOGAMY

THE flowers of *Antirrhinum majus* are too well known to require description, and while those of *A. glutinosum* differ in size and in pigmentation, they are of the same general shape, structure and development. The F_1 hybrid between those species has its own typical size of flower, intermediate between those of the parents though nearer to *A. majus*, but once again the shape, structure and development is of the same general kind (see Mather, 1947, plate I).

At the bud stage in both the species and their hybrid the upper lobes of the corolla limb are folded over the lower so that the mouth of the corolla tube is completely sealed. When the flower opens both the upper and lower parts turn back, so that although the entrance to the corolla tube is still no more than a slit, visiting bees can alight on the lower lobes and force their way into the tube. The reproductive organs are protected from the weather, but bees can gain access to them and effect pollination.

Visits by bees are not essential for pollination in at least most strains of *A. majus*. Even when the insects are excluded by bags the flowers will set a crop of seed. Evidently the pollen can reach the stigma of the same flower without the intervention of any external agency. Nevertheless, when bees are allowed free access to the flowers, interchange of pollen does occur between the flowers of different plants and also, one must presume, between flowers of the same plant. In a mixed stand of approximately equal numbers of two strains of *A. majus*, distinguished by marker genes whose effect on flower colour enabled hybrids to be recognised, Mather (1947) found that natural pollination resulted in 12 per cent. inter-strain hybrids. Assuming that transference of pollen from one plant to another of the same strain was as likely as transference to a plant of opposite strain, we can estimate that on the average 24 per cent. of the seed set by each flower was from fertilisation by pollen from a different plant. The remaining 76 per cent. of the seed must have been the outcome of self-pollination within the flower, or of its genetical equivalent, the interchange of pollen between flowers of the same plant.

In *A. glutinosum* cross-pollination between plants not merely occurs, but is almost essential for seed setting. The species possesses an incompatibility mechanism of the type found for example in *Nicotiana*, sweet cherries and clover (see Lewis, 1949). The incompatibility is not quite complete ; when sufficient flowers are self-pollinated out of doors some seed is obtained, and in the greenhouse capsules have been obtained from as many as 38 per cent. of the flowers so treated. Under these special conditions, self-pollination, and with it, of course, cross-pollination between plants having the same genotype in respect of the incompatibility, can lead to some seed setting ; but under the conditions of natural pollination, when the incompatible pollen will be in competition in the style with the compatible, the proportion of seed resulting from self-pollination must be negligible.

Thus both the species *A. majus* and *A. glutinosum* show cross-pollination as a result of visits by bees ; in one of them a quarter of the seed comes from this source and virtually all of it in the other. One is a facultative and the other an obligatory cross-breeder.

Nine different inbred strains of *A. majus* have been crossed with *A. glutinosum*. During the seven years 1943 to 1949, a total of 786 plants have been raised by selfing within these strains taking all of them together. None of these plants has shown any indication of abnormality in the opening of its flowers though some abnormality of the shape of the corolla, and distortion of the anthers has been seen at times in two of the strains, and petaloidy of the anthers in a third. These abnormalities in no way resemble the cleistogamy which is described below. Of some thousands of non-inbred *A. majus* plants raised during the past nineteen years none has been observed to show any abnormality resembling this cleistogamy.

Over the same period of seven years 293 plants have been raised of normally cross-bred *A. glutinosum*, excluding inbred lines. The plants have all had normal flowers. In inbred lines some plants have tended to have abnormal corollas somewhat reminiscent of the cleistogamous type. These would, however, never be confused with the true cleistogamous type nor even with the partially cleistogamous which will be described. They are abnormal mainly in having the limb of the corolla much reduced.

The nine F_1's of the species cross have included between them 679 plants, all of which have had perfectly normal flowers. The F_2's, however, have included in their total of 1397 plants, 6 with flowers of the cleistogamous type. These 6 plants occurred in three different F_2's as shown in table 1. There is nothing to indicate that the remaining six crosses were incapable of giving cleistogamous plants in F_2. Indeed, very large families would be required to demonstrate that the nine F_2's differed in this respect. We have therefore pooled all the crosses in considering the frequency of occurrence of cleistogamy. Should differences exist between the families we shall have underestimated the frequency of cleistogamy in the families where it can occur.

With six cleistogamous plants out of 1397, the frequency is 0·43 per cent. If cleistogamy had been as likely in the parents and F_1's as in F_2, we should expect to have found 3·38 such plants among

TABLE 1

The incidence of cleistogamy in A. majus, A. glutinosum *and their cross* (1943-49 *inclusive*)

A. glutinosum—293 plants, all normal

	A. majus Plants all normal	F_1 with *A. glutinosum* Plants all normal	F_2	
			Normal	Cleistogamous
Line 1	81	34	155	0
2	80	83	222	2
3	90	81	148	0
4	81	52	115	1
5	76	87	171	0
6	94	76	170	3
7	96	72	115	0
9	80	94	137	0
10	108	100	158	0
Total . .	786	679	1391	6

the 786 individuals of *A. majus*, 1·26 among the 293 *A. glutinosum*, and 2·92 among the 679 F_1's. No such plant was in fact found. The differences in frequency of cleistogamy between parents, F_1 and F_2 are not, however, significant when the two parents and F_1 are compared separately with F_2 by contingency χ^2's using Yates' correction for continuity. If parents and F_1 are pooled, to give a total of 1758 plants none of which was cleistogamous, the difference between the pool and the F_2 is just significant ($\chi^2_{[1]} = 5{\cdot}471$, $P = 0{\cdot}02$). It may be noted that even if the three segregating F_2's are compared, as a group, with their three parental strains of *A. majus*, or with their corresponding three F_1's, the differences in frequency are not significant.

There is thus no final statistical evidence that the frequency of cleistogamy in the species F_2 is higher than in the parental species. The difference between F_2 on the one hand and the pool of parents and F_1 on the other is admittedly significant, but the validity of such pooling may well be questioned. It should, however, be remembered that the 786 plants of the parental strains of *A. majus* are only a small fraction of the many thousands of individuals of this species which have been grown during the past nineteen years, and no plant with cleistogamous flowers has been recorded. It is therefore unlikely that this cleistogamy in the species F_2 is merely a reflection of a similar phenomenon in the parent strains of *A. majus* which has escaped detection by the hazards of sampling.

The evidence in respect of *A. glutinosum* is less good. Though some inbreds have been grown additional to the 293 normally cross-

bred plants, our experience with this species is much smaller than that with *A. majus*. The most that can be said is that although some floral abnormalities have been observed in inbred material, nothing which could properly be termed cleistogamy has been seen in this species up to the present.

2. GRADES OF CLEISTOGAMY

Fully cleistogamous flowers differ in two chief ways from those which are normal for the parent species and F_1. Both upper and lower lobes of the corolla limb are much reduced in size (a character which is shared with some inbred plants of *A. glutinosum*), and the upper lobes never turn back, so that even when fully developed the entrance to the corolla tube is closed by the limb (which has not been seen even in inbred *A. glutinosum*). Cleistogamous flowers are also often smaller in overall size than even the *A. glutinosum* parent. The calyx and the internal parts, stamens and pistil, seem, however, to be as well formed as those of the normal flower. So far as can be judged from simple inspection, the pollen of a cleistogamous flower is good. A cleistogamous flower is illustrated on the right of plate I.

Plants which bear cleistogamous flowers also differ from the normal in their foliage. Growth is very compact and bushy and the leaves are small, convex and closely set on the stems, especially near the tips. This " pin-cushion " habit, reminiscent of many rock plants, is especially noticeable during the first year's growth of the plant. If kept for a second year there is a tendency to show a more normal habit. Pin-cushion growth is shown in the lower part of plate III.

Grades exist of vegetative, as well as of floral, differences from normal. In regard to the flowers we have found it convenient to recognise five grades of abnormality. In two of these (1 and 2) the flowers can be described as near normal, their main departure being some reduction in size of the corolla limb whose edges are also curled more than usual. Grade 3 we have described as partial cleistogamy. In it the upper limb of the corolla fails to turn back properly so that the mouth of the corolla tube is partly blocked ; but the blockage is not so complete, nor presumably so effective as in the fully cleistogamous flower. In grade 4, which we have called near cleistogamy, the flowers of one plant may include some which are fully cleistogamous (grade 5), but will also include others which are nearer to grade 3. Some of the types of flowers and plants are shown in plates I and III, which will illustrate the classification adopted better than a verbal description.

It will be seen from the description of grade 4 that the flowers of one plant may vary amongst themselves at one time. There may also be some variation with the progress of the season, the earlier flowers tending if anything to be a little more cleistogamous than the later ones. This variation has at times led to revision of the classification

of a plant, but never by more than one grade. The classification in one year can thus be regarded as reliable to within one grade. When kept for more than one year, the second season's flowers of a cleistogamous plant have been noticeably less cleistogamous than the first season's.

Six grades of leaf type have been recognised. Three of these are the two parental (which of course differ) and the F_1 types (plate II and plate I in Mather, 1947). Our grade D is similar to *A. majus* but with the leaves reduced and narrower though without the dense pin-cushion type of growth. Grade E has much reduced leaves and a more nearly pin-cushion habit, while grade F is the type which characteristically can bear fully cleistogamous flowers (plate III).

There is not a complete correlation between the grades of floral and vegetative variation. Fully cleistogamous plants (grade 5) have never been seen to be other than grade F vegetatively. Partial cleistogamy and even near cleistogamy (grades 3 and 4) may occur with vegetative development of types D and E as well as F and even at times with grade C, similar to the species F_1. Near normal flowers may be associated with any type of foliage, and normal flowers have been seen on plants with all types of vegetative development except grade F. These observations are summarised in table 2. It should

TABLE 2

Leaves \ Flowers	Normal	1 and 2	3	4	5
A and B	+	+	−	−	−
C	+	+	+	−	−
D	+	+	+	+	−
E	+	+	+	+	−
F	−	+	+	+	+

+ = combination observed
− = combination not observed

be noted, of course, that in the case of full cleistogamy, inspection of more plants than we have been able to raise up to the present might reveal the possibility of grade 5 flowers being associated with less extreme pin-cushion foliage. No such observation has, however, yet been made.

3. THE CONSEQUENCES OF CLEISTOGAMY

Pollination is normally effected by bees in both *A. majus* and *A. glutinosum*. The bee forces its way in through the mouth of the corolla tube and, when inside, its dorsal surface must come into contact with both anthers and stigma. Self-pollination seems inevitable from the positions of anthers and stigma, which mature at the same time ;

and, of course, cross-pollination must also occur as the bees move from the flowers of one plant to those of another. In *A. glutinosum*, incompatibility places the pollen from the same plant at a disadvantage on the stigma and the seed is preponderantly, if not entirely, from cross-pollination. In *A. majus* on the other hand, incompatibility plays no part, with the result that most of the seed is from selfing, about a quarter coming from crossing (see above). In *A. majus* selfing can, and indeed commonly does, occur without the intervention of bees, as when these are excluded by protective bags.

Full cleistogamy appears to be effective in denying bees entry into the corolla tube. Bees have been seen endeavouring to gain entry into such flowers on a number of occasions, but never successfully. Thus any seed set naturally by a fully cleistogamous flower will be by self-pollination without an insect vector. This is perhaps less regularly true for a partially cleistogamous flower, or even possibly for a near cleistogamous. Nevertheless full cleistogamy, even if not partial cleistogamy, must be regarded as a means of securing regular inbreeding.

Granted, however, that seed from fully cleistogamous flowers must be by self-pollination, two further questions arise in considering cleistogamy as an inbreeding mechanism :—(i) can such flowers pollinate themselves without outside intervention, and (ii) would such pollination be effective, or would it on the other hand be vitiated by incompatibility or sterility? Experimental evidence is available on these points.

Tests were conducted in 1947, 1948 and 1949 of the ability of plants having cleistogamous flowers of various grades, to set seed when insects were excluded. Self-pollination was ensured by artificial means in some flowers, while others were left to pollinate themselves naturally. The tests of 1947 were not comparable with those of the later years in that observations were not made on individual flowers but were confined to recording whether whole inflorescences set one or more capsules as opposed to failing entirely to give seed. In 1948 and 1949 the numbers of flowers were observed which set capsules after treatment in the one way or the other.

In 1947 four plants, two fully and two partially cleistogamous, were covered by cages. The flowers on some inflorescences of each plant were self-pollinated by hand while those of others were left to self-pollinate themselves. No consistent difference was observed in the proportion of inflorescences setting at least one capsule following the two treatments (table 3A). A difference appeared, however, between the cleistogamous and partially cleistogamous plants. Of 18 inflorescences on the former, 7 bore at least one capsule. Of 19 inflorescences in the partially cleistogamous plants, 16 bore at least one capsule. The cleistogamous plants were less successful than the partially cleistogamous in setting seed whether artificially self-pollinated or not (Mather, 1948).

The results of the tests made on individual flowers in 1948 and 1949 are shown in table 3B.

TABLE 3A

Seed setting following artificial self-pollination (A) *and undisturbed natural self-pollination* (N) *in cleistogamous plants guarded from insects*

Type of plant	Inflorescences		Total
	A	N	
Partially cleistogamous . . .	10/11	6/8	16/19
Cleistogamous	2/8	5/10	7/18
Total . . .	12/19	11/18	

TABLE 3B

Grade of cleistogamy	3		4		5	
Type of pollination	A	N	A	N	A	N
1948	2/37	1/24	0/1	0/1	1/15	0/16
1949	1/8	1/9	0/3	0/2	0/1	...
Total . . .	3/35	2/33	0/4	0/3	1/16	0/16

The figures show (in table 3B) the number of capsules set over the number tested, and (in table 3A) the number of inflorescences setting at least one capsule over the number of inflorescences tested.

Again there is no good evidence that natural pollination is less successful than artificial. It might be said that there is a hint of such a difference, but any inadequacy of natural pollination is certainly small as a cause of reduction in seed setting when compared with the other causes of sterility so obviously at work in these plants. As we have seen, the results from the cleistogamous plants of 1947 lend no support to such a difference.

It will be noted that, as in 1947, the partially cleistogamous flowers set more capsules than the cleistogamous. Taking all pollinations on grade 3 plants, 5 capsules set out of 68 flowers, while grades 4 and 5 pooled gave 1 capsule out of 39 flowers. These results are not significant by themselves, but when combined with those of 1947 the trend seems reasonably clear.

There is thus no evidence that the mechanism of natural self-pollination is badly inadequate. The cleistogamous plants set few seeds but not on account of failure of self-pollination by natural means. Other causes must be at work and these might spring from self-incompatibility inherited from the *A. glutinosum* parent, or from

genuine sterility due to genic unbalance. Certain crosses, made particularly in 1948, throw some light on the position. The results of these crosses are set out in table 4.

TABLE 4

Results of crosses with the cleistogamous types

Female \ Male	Cleist. of grade 3	Cleist. of grade 4	Cleist. of grade 5	*A. majus*	*A. glutinosum*
Cleist. of grade 3	5/11	0/1	0/1	2/4	1/1
Cleist. of grade 4	...	...	...	...	...
Cleist. of grade 5	3/6	...	0/1	1/1	...
A. majus	2/3	0/1	1/1	...	...
A. glutinosum	4/9	...	...	...	...

All crosses among cleistogamous parents 8/20.
All crosses of cleistogamous and species 11/20.
The results are given as number of capsules set over number of flowers pollinated.

There is no good indication in the table that the seed setting of the crosses with the parent species differed according to whether the species was male or female or that crosses with one parent species were more successful than those with the other. We can thus pool all the crosses of cleistogamous plants with the two parental species to find 11 successful pollinations out of 20 made. This is a markedly higher proportion of successes than that obtained when the cleistogamous plants were self-pollinated. Furthermore, the result of intercrossing cleistogamous plants, as shown by table 4, was 8 successes out of 20 pollinations. This proportion of successes is nearly as high as that from the species crosses, and is significantly higher than the proportion of successes, 6 out of 107, achieved by selfing the cleistogamous plants as shown in table 3B ($\chi^2_{[1]} = 16{\cdot}97$). Even if, in order to make a more rigorous comparison we confine our attention to the behaviour of grade 3 plants, we find 5 successes out of 11 intercross pollinations between such plants while there were only 5 successes out of 68 flowers self pollinated. This gives the highly significant $\chi^2_{[1]} = 9{\cdot}23$ after applying Yates' correction.

Most of these tests of the behaviour of cleistogamous plants were made in 1948. In that year, 8 grade 3 plants were tested for seed setting ability following artificial and natural self-pollination. Eight were also used in the tests with cross-pollination, 6 of the plants being common to the self and cross-pollination tests. There is thus no great likelihood that the difference in success of self and cross- pollination is to be traced to the individual vagaries of behaviour in the plants used. It seems that cross-pollination, whether with other cleistogamous plants or with the parent species, is more successful in setting seed than is self-pollination in the cleistogamous types.

About 50 per cent. of the crosses made were successful in that the flower set a capsule. Mather (1947) records that in an extensive test carried out during 1943 the success of crosses within and between the parental species was as shown in table 5.

TABLE 5

Percentage of successful cross-pollinations within and between the parent species (Mather, 1947)

Parent: Male / Female	*A. majus*	*A. glutinosum*
A. majus . . .	93 per cent. (15)	72 per cent. (96)
A. glutinosum . . .	47 ,, (32)	35 ,, (20)

The figures in brackets after the percentages are the numbers of flowers pollinated.

The percentage success is lower in the present tests of cleistogamous flowers than in these earlier tests of *A. majus* females, whether with *A. majus* or *A. glutinosum* pollen; but the results from *A. glutinosum* mothers are very similar to those from the cleistogamous plants. Further, *A. glutinosum*, being self-incompatible set capsules from only 4 per cent. of its flowers self-pollinated in 1947. This compares with 7 per cent. after self-pollination of grade 3 plants and 2·5 per cent. after self-pollination of grade 4 and 5 plants (table 3). The grade 3 plants are thus the equal of *A. glutinosum* in fertility whether crossed or selfed, and even the grade 5 plants are only little inferior.

We can now give an answer to the question whether the poor set of capsules following the self-pollination of cleistogamous plants is due to incompatibility or true sterility. The grade 3 plants are no less successful in capsule setting than is the parent species *A. glutinosum*. Like *A. glutinosum* the grade 3 plants set fewer capsules after selfing than after crossing and this, we presume, must be due to incompatibility inherited from this parent species. Grade 3 plants are not so successful in crosses as *A. majus*, but even if this should be taken as indicating some sterility (at least under London conditions) the degree is no greater than that shown by *A. glutinosum*.

The fully cleistogamous plants of type 5 are less successful after self-pollination than are those of grade 3, and possibly also a little less successful after crossing. Thus they show the same incompatibility as *A. glutinosum* and grade 3 and they may well also suffer the handicap of some genuine sterility.

4. THE INHERITANCE OF CLEISTOGAMY

The cleistogamous plants whose breeding behaviour was followed arose in the F_2 of the cross of *A. glutinosum* with *A. majus* strain 6.

Three such plants appeared in 1945, two being fully, or at least near cleistogamous, and the third a partial cleistogamous (it was described at the time—before the numerical grades were introduced—as half way between normal and cleistogamous). This partially cleistogamous plant was not bred. The other two fully cleistogamous plants were self pollinated. One gave 6 offspring, all cleistogamous like the parent, which were bred no further, or at least gave no seed. The other gave 8 offspring, all cleistogamous. One of these was selfed and gave three offspring, two of which failed to flower, the third being cleistogamous like its parent. On selfing, this third plant gave some seed which, however, failed to germinate when sown in 1948. All these cleistogamous plants, both the two parents and their descendants, had pin-cushion foliage.

At the same time as the two original cleistogamous plants of 1945 were self-pollinated, 7 of their normal sibs in the F_2 were also selfed. Of these 5 gave respectively 10, 10, 9, 9 and 2 normal offspring. A sixth plant gave 2 normals, 1 cleistogamous and 1 which did not flower; and the last gave 7 normals and 1 cleistogamous. None of these was bred further. These breeding results from the F_2 plants are summarised in table 6.

TABLE 6

Breeding behaviour (by self-pollination) of normal and cleistogamous plants in F_2 and F_3 of the species cross

Parent plants		Offspring		
		Normal	Cleistogamous	Not flowering
1945	Cleistogamous	0	8	0
	Cleistogamous	0	6	0
	Five normal (pooled)	40	0	0
	Normal	2	1	1
	Normal	9	1	0
1946 Cleistogamous (ex 1st family above)		0	1	2

The last of the selfed cleistogamous lines, which had given nothing but cleistogamous and non-flowering plants, failed after 1947. The plants grown since that date mostly trace back to a cross made between the two original cleistogamous plants in the F_2 of 1945. This family, 79/1946, contained 10 plants, consisting of 2 normal, or nearly so, 3 partially cleistogamous and 5 fully cleistogamous. The breeding behaviour of this line is shown in table 7.

Several remarkable things appear from this table. In the first place no member of this line bred true for full cleistogamy, even though families were grown from a fully cleistogamous individual in 1947, 1948 and 1949, as well as from partially cleistogamous individuals.

Indeed there is little evidence that the fully cleistogamous parent produced families (164/47, 166/48 and 43/49) more cleistogamous

TABLE 7

Breeding behaviour in the line descended from the cross between the cleistogamous plants in the F_2 of 1945

Family	Parent			Offspring					
				Grade					Not flowering
	Origin	Grade	Pollination	N	1 and 2	3	4	5	
79/46	Original cross			2		3	5		...
164/47	79/46	Cl	S	3		7	1		...
166/48	164/47	Cl	S	...	2	11	4	...	2
43/49				...	...	1	...	...	...
163/48	164/47	P. Cl	S	...	5	1	1	1	...
164/48	164/47	P. Cl	S	...	4	14	3	2	7
49/49				...	8	2	...	...	7
152/49	163/48	2	O	13	5	...	...	...	...
78/49	,,	4	O	15	3	...	...	...	...
53/49	164/48	3	S	12	8	...	...	...	...
54/49	,,	3	S	3	5	...	...	...	4
79/49	,,	3	O	1	9	4	...	...	1
80/49	,,	3	O	19	1	...	...	...	...
81/49	,,	3	O	16	1	...	...	...	...
82/49	,,	3	O	19	...	...	...	...	...
83/49	,,	3	O	13	5	...	1	...	...
84/49	,,	2	O	14	6	...	...	...	...
85/49	,,	1	O	16	4	...	...	...	...
86/49	,,	3	O	16	4	...	...	...	...
87/49	,,	2	O	1	1	...	...	...	...
48/49	166B/48	3	S	7	3	2	...	...	1
77/49	,,	3	O	3	1	...	...	...	...

Cl = fully cleistogamous (= later grades 4 or 5)
P. Cl = partially cleistogamous (= later grade 3)
S = self pollination
O = open pollination

on the average than the partially cleistogamous parents (families 163/48, 164/48, 49/49). It does appear, however, that before 1949 the line bred true for the occurrence of cleistogamy of greater or lesser grade.

In 1949 there was less cleistogamy than in earlier years and the grade of such cleistogamy as occurred was generally lower. Many of the families grown in 1949 were admittedly from open pollination of cleistogamous plants in the previous year. This seed was used to ensure the maintenance of cleistogamy following the poor success of self-pollination in 1948. On the whole, normal offspring are

more frequent (as compared with grades 1 and 2) in these families from open pollination than in those from selfing. This is fairly attributable to the natural crossing that would presumably occur even in grade 3 plants (as these have flowers which are not completely closed at maturity) and which would be at an advantage as compared with self-pollination. Even the families from known self-pollination contained, however, a great proportion of plants with normal flowers and a low proportion of grades 3, 4 and 5. Evidently cleistogamy manifested itself less clearly in 1949 than in earlier years, a difference which we may perhaps relate to the change of location of the crop from London (where it was grown in 1948 and earlier) to Birmingham (where it was grown in 1949). The duplicate families 164/48 and 49/49 confirm this difference. The environmental effect is in fact greater than the genetical difference between the fully and partially cleistogamous parents of 1947.

The line just described was from a cross between the two cleistogamous plants in the F_2 of 1945. The reciprocal of this cross was allegedly made, but the seed so obtained gave, in 1946, a family of 10 plants all like *A. glutinosum*. One of these plants on selfing gave 10 offspring in 1947, again all like *A. glutinosum*. A second plant of the 1946 family was crossed with the single fully cleistogamous plant of 1946 recorded in table 6. The offspring of the cross included 7 plants with normal, 3 with partially cleistogamous and 1 with fully cleistogamous flowers. These results suggest strongly that as a result of some slip the original cross of 1945, from which all the plants described in this paragraph were descended, was not cleistogamous × cleistogamous as supposed, but cleistogamous × *A. glutinosum*.

However this may be, the single grade 5 plant of 1947 was selfed and gave in 1948 1 grade (3), 3 grade (4), 5 grade (5) and 5 not flowering. A duplicate of this family, grown in 1949 from stored seed, gave 2 grade (2), 3 grade (4), 2 grade (5) and 3 not flowering, again suggesting less cleistogamy in 1949 than in 1948. The grade (5) plant of 1947 seems on this evidence to have been breeding true to cleistogamy even if not to a particular grade. A further family from the self-pollination of a 1948 grade (4) plant which gave in 1949, 14 normal and 5 grade (1) plants. As in the other crossed line, described earlier, the semblance of breeding true for cleistogamy in 1948, vanished in 1949. The environmental effect obscures the genetical situation and makes confident interpretation impossible.

Crosses were made between cleistogamous plants and the parental species in the hope of learning something of the inheritance of cleistogamy. The results are summarised in table 8. It will be seen that the cross allegedly between the two cleistogamous plants of 1945, but now believed to have been of the cleistogamous mother by *A. glutinosum* has been included as of this latter kind but marked with an asterisk. With a few exceptions all the F_1's of cleistogamous by both species had normal flowers, close in type to those of the species

used in the cross. A single plant out of 80 grown in 1949 from cleistogamous × *A. majus* was of grade 1, *i.e.* just not quite normal. A further family in 1949 from cleistogamous × *A. glutinosum* was recorded as

TABLE 8

Crosses of cleistogamous (cl) *with the parental species* A. majus (m) *and* A. glutinosum (gl)

Cross	Family	Offspring					
		Grade					Not flowering
		Normal	1 and 2	3	4	5	
cl × *m*							
F_1	162/48	26	...	...	...	...	...
	56/49	20	...	...	...	...	...
	57/49	20	...	...	...	...	...
	58/49	19	1	...	...	...	...
	60/49	20	...	...	...	...	...
F_2 (from 162/48)	74/49	30	1	...	...	...	...
F_1 (from 162/48) × *m*	63/49	19	...	...	...	...	...
F_1 (from 162/48) × *cl*	64/49	14	5	...	...	...	...
	65/49	11	6	2	1	...	...
cl × *gl* (normal)							
F_1	81/46*	10	...	...	...	...	...
	165/48	30	...	...	...	...	...
	167/48	10	...	...	...	...	...
F_2 (from 81/46)	162/47*	10	...	...	...	...	...
F_1 (from 165/48) × *gl*	66/49	[19	1]	...	...	...	...
F_1 (from 167/48) × *gl*	88/49	20	...	...	...	...	...
gl × F_1 (from 167/48)	68/49	[18	2]	...	...	...	...
	69/49	[15	5]	...	...	...	...
F_1 (from 81/46) × *cl*	163/47*	7		3	1		...
gl (inbred) × *cl*							
F_1	159/48	10	8	...	...	...	...
	62/49	[9	11]	...	...	...	...
F_2 (from 159/48)	71/49	2	24	4	...	...	...
	72/49	6	7	3	1	...	1

* From cross in 1945 inferred to be *cl* × *gl*.

[ ] Grade 1 plants so near normal that validity of distinction doubtful.

having 9 normally flowered and 11 grade (1) flowered plants; but the two kinds were so similar that the distinction between the two classes was very difficult to draw. This family qualifies but little the general statement that the F_1's with the species have normal flowers. The genes associated with cleistogamy are recessive to, or of low joint potence as compared with, those brought in from the parents. Indeed, only one F_1 family requires special mention, viz. 159/48. This definitely included plants with non-normal flowers. It was a cross between a cleistogamous and an inbred line of *A. glutinosum* and as

we recorded in Section 1, our inbred lines of this species departed from the type by often having a reduced corolla. It may be, therefore, that this exceptional behaviour is also reflected in the F_1 with cleistogamy, the genes coming in from the inbred line being more similar to the genes of the cleistogamous line.

In the only F_2 grown from the cross with *A. majus* 1 plant out of 31 departed slightly from the normal type of flower. There is thus little evidence of segregation since a single departure was also observed in F_1. The backcross of the F_1, from $cl \times m$ to *A. majus* gave, as might be expected, nothing but normally flowered plants in the family of 19 which was grown. The backcross of this same F_1 to cleistogamous showed segregation. Of 19 plants, 5 were not normal and 3 of these at least departed sufficiently from the normal flower type of the species for there to be no doubt that cleistogamy was manifesting itself once again. In the case of a second family from backcrossing to *cl* the evidence is even stronger. Only 11 plants of 20 had normal flowers and 3 fell into grades 3 and 4. It is worth while noting too that these families were grown in 1949 when the manifestation of cleistogamy was, in general, poor.

The later generations of the cross with *A. glutinosum* require consideration in two parts. The F_2 of the cross made in 1945, and now believed to be with *A. glutinosum*, was of 10 plants, all like the species. No segregation was apparent. Equally the four backcrosses of F_1's from later crosses between *cl* and standard *A. glutinosum* (66, 68, 69 and 88/49) gave little evidence of segregation for cleistogamy. Of 80 plants, 8 were regarded as having not quite the normal type of flower for the species, but they departed so slightly from the species type as to leave considerable doubt whether they should be regarded as a distinct class. Only one backcross to *cl* has been grown and that from the putative F_1 in 1946. This gave 7 normal and 4 partially or fully cleistogamous plants.

The second group of descendants were true F_2 families for the cross with inbred *A. glutinosum* to whose F_1 (159/48) special attention has already been drawn. This F_1 contained non-normally as well as normally flowered plants. The F_2's were from two non-normal individuals and 47 plants which flowered gave 8 in grades 3 and 4 and only 8 classified as normal. This is in clear contrast to the other descendants of the cross with *A. glutinosum* and shows, together with the F_1 data that the inbred line of *A. glutinosum* differed from the standard lines in its content of the genes related to cleistogamy. The greater proportion of cleistogamous individuals in the descendants of the inbred line suggest fewer gene differences between this line and cleistogamous than between type *A. glutinosum* and cleistogamous.

Confident interpretation of these various pieces of evidence on the inheritance of cleistogamy is made difficult by the non-heritable modification of the expression of cleistogamy. It is particularly difficult to relate the observations made in 1949 to those of earlier

years. If we neglect the 1949 results the data of tables 6 and 7 suggest strongly that the early cleistogamous lines bred true to cleistogamy of one grade or other, even if not to a particular grade. The 1949 results may be accommodated with this view if we postulate that conditions in Birmingham during 1949 did not consistently lead to the development of cleistogamy from genotypes which would consistently have given this flower form (in greater or lesser degree) had they developed under the London condition of earlier years. And we should remember that cleistogamy was, in fact, detected and selected under the earlier conditions, so that had the original species F_2's been first produced in Birmingham in 1949 we might well never have recognised the phenomenon. The lines bred true under the conditions in which cleistogamy was detected : their phenotypes failed in consistency under new conditions.

The variation of grade in the crossed line in its early years also seems to have been largely non-heritable, for such partially and fully cleistogamous plants as were tested bred alike. There would seem, however, to have been some genetical modification of grade, for the families of table 6 (in the lines descended by self-pollination from the first cleistogamous plants) contained only fully cleistogamous individuals, while those of table 7 (from the crossed line) contained more partially than fully cleistogamous plants. This difference is not to be attributed wholly to different conditions or finer classification arising with increasing familiarity with the phenomenon, since the first crossed family was grown side by side with progenies obtained by selfing its parents, the difference in grade between them being observed and recorded at that time. There must be a genetic element in the determination of grade, though no precise statement about it is possible. There is even a suggestion that the cleistogamous families segregated (in 1947 and 1948) from the probable cross of one of the first such plants with *A. glutinosum* had their own characteristic balance of grade, with more of grade 4 and 5 than the crossed line but less than the original selfed lines.

Assuming that the results of 1949 are obscured by the changed conditions and that the lines bred true to a basic genotype giving consistent cleistogamy (though of genetically modifiable grade) under the conditions of earlier years, we must next enquire as to the nature of this basic genotype, leaving aside for this purpose consideration of the grade modifiers. Here our difficulties increase because most of the segregating families from the crosses with the parental species —and it is these crosses which would tell us most—were grown in 1949.

The crosses with both the parental species show segregation in backcrosses to cleistogamous though not in backcrosses to the species. A minimum of two recessive genes must thus be involved in the primary genotype of cleistogamy, one differentiating it from each species. The backcross ratios are not wholly incompatible with this minimal postulate, though in general more normals are found in

the backcrosses than the simple half which would be predicted on this view. The original segregation of cleistogamous individuals in the F_2 of the species cross also throws doubt on the adequacy of the two gene hypothesis for, even excluding F_2's in which no cleistogamous plants were found, the ratio of normal : cleistogamous was 507 : 6 or 84·5 : 1—a ratio hard to reconcile with the 15 : 1 expected. Even allowing for the effects of grade modifiers and the possibility that very low grade cleistogamy was overlooked in the early years, it is difficult to believe that only two primary genes are involved. Three, however, would be sufficient to account for the segregation observed.

The crosses of cleistogamous to inbred *A. glutinosum* suggest that this latter line may differ from cleistogamous in fewer genes than does normal *glutinosum*. If we are prepared to admit three primary genes, normal *A. glutinosum* might differ from cleistogamous in two (of which one might be heterozygous) and inbred *glutinosum* in one. It would be necessary to suppose that the gene by which the inbred line differed from the type *A. glutinosum* had a reducing effect on the corolla, for the inbred line itself shows this departure from type. The postulation of this effect would serve further to explain the low number of normals in the F_2 of cleistogamous $\times$ inbred *A. glutinosum*, for such a phenotype would easily be confused with low-grade cleistogamy. It would indeed, in a sense, be low-grade cleistogamy requiring further supplementary genes to enhance it.

Thus the genetical architecture of cleistogamy, though not clearly established, must be of some complexity. A number of genes must be involved, some supplementary in action and primarily concerned in giving cleistogamy as opposed to normal flower type : others perhaps modifying the grade of cleistogamy, where the primary genotype gives this departure from normality. Furthermore, none of the genes has an effect which is great as compared with the environmental and developmental differences observed in the experiments. The system involved is not a polygenic system in the strict sense, but it has some of the latter's properties, and in particular it is one which can give rise to grades of expression of the character.

5. CLEISTOGAMY AS AN INBREEDING MECHANISM IN *ANTIRRHINUM*

It is clear that seed set sexually by fully cleistogamous flowers in any species of flowering plants, must be the result of self-pollination. Cleistogamy is therefore an inbreeding device. While our lower-grade cleistogamous flowers in *Antirrhinum* may well permit the ingress of bees and so give some seed by cross-pollination, the grade 5 and even grade 4 plants must be regarded as showing this inbreeding mechanism. Thus the two parental species, one an obligatory cross-breeder and the other regularly setting a considerable fraction of its seed by cross-pollination, contain between them all the genetical

materials necessary for the production of an inbreeding type of plant, *i.e.* a type of plant with a breeding system distinct from, and even opposed to, those of its parents.

A successful change from cross-breeding to inbreeding must, however, involve more than the mere development of a device, such as cleistogamy, which precludes cross-pollination. The plants must be capable of setting as good a crop of seed by inbreeding as their predecessors did by cross-pollination and these inbred offspring must not be so genetically incapacitated as to be at a disadvantage in competition with the hitherto normal cross-bred types. Indeed, they must be at a slight advantage in the particular environment if the inbreeding mechanism is to spread and become more than a chance, or floating, novelty.

That these conditions can be fulfilled is attested by the rise of inbreeding devices that must be inferred in many species of plants—wheat, peas, chickweed and so on. Even *A. majus* itself seems to have moved towards inbreeding as compared with its relatives such as *A. glutinosum* and *A. molle*, though it is by no means a complete inbreeder. The extreme cleistogamous type which has arisen in our experiments is mechanically such a complete inbreeder, but it could not in its present form be regarded as representing a biologically successful move towards complete inbreeding.

The pollination mechanism of our cleistogamous plants is mechanically successful, in that natural pollination gives rise to as many capsules as does deliberate selfing. Biologically, however, it is not successful. The cleistogamous plants appear to have inherited the self-incompatibility of their *A. glutinosum* parent, and the cross-breeding device is not overcome by the cleistogamy. Indeed, the combination of the two results essentially is a great reduction of seed set, since one device precludes cross-breeding and the other precludes, or at least materially reduces, inbreeding.

The incompatibility mechanism is not, in itself, a final obstacle. Incompatibility mechanisms can be broken down (Mather, 1943*a*). Indeed self-compatibility does exist in the genus and, in the case of *A. majus*, may well have supervened on incompatibility. It is, however, clear that if cleistogamy were to become a workable mechanism for regular inbreeding, its rise must be accompanied, or preceded, by the destruction of self-incompatibility. So far as the physiological relations of pollen and style are concerned, cleistogamy could be successful in *A. majus* but not in *A. glutinosum* as at present constituted.

In addition to this need for a physiological readjustment of pollen and style coordinated with the mechanical change in pollination—a need which, though widespread, would not be encountered in all cases of movement from cross-breeding to inbreeding—there is another necessary adjustment and one which will always be concerned in such a change of breeding system. This is the genetical readjustment necessary for the avoidance (or material reduction) of the inbreeding

depression which is a universal feature of cross-breeding species. The property of poor internal balance is one which must be shown by the combinations of virtually all the systems of genes in a cross-breeding species (see Darlington and Mather, 1949). The readjustment towards that good internal balance of the genic combinations, by which inbreeding is permitted without depression of vigour and fertility, must thus be complex and therefore slow ; and if the rise of an inbreeding mechanism should outstrip the rise of this general genetical readjustment, the mechanism will be to that extent put at a disadvantage, by the poor capacity of the offspring it produces. On the other hand, good internal balance will not be achieved without inbreeding, for only by inbreeding will the homozygous types be exposed regularly to the natural selection which will pick out the balanced combinations of genes. Only where breeding mechanisms and internal genetic balance rise together in a coordinated way can success be achieved. The high fitness, which inbreeding can give and which is the advantage of inbreeding (Mather, 1943*b*), requires not merely uniformity, but uniformity at a highly adjusted genetical level, and it is this which will govern the pace of the change from outbreeding to inbreeding. The changes in breeding system and balance must be kept in step and the steps must therefore be small.

A change towards inbreeding in the species of *Antirrhinum* with which we are concerned, would constitute no exception to this rule. The effects of inbreeding in *A. glutinosum* are as clear and drastic as is expected in a crossbreeder. Even in *A. majus*, where cross-breeding is neither obligatory nor predominant, inbred lines are generally less vigorous and more prone to developmental upset than normally open-bred populations, with which they could not, therefore, compete on even terms. They are not, however, so much incapacitated as in *A. glutinosum*, and this, together with the absence of incompatibility, suggests that *A. majus* may have changed and indeed be in the process of changing, towards inbreeding. Incompatibility and poor internal balance are not invariable with the genus and cannot therefore be final obstacles to successful inbreeding within it.

Thus in *Antirrhinum* as elsewhere the rise of an inbreeding mechanism would be contingent on a coincidental readjustment of the general genetic balance, as well as the genetical abolition of any initial self-incompatibility. That these changes are to be regarded as practical possibilities is attested by behaviour within as well as outside the genus. Our observations show that the genic materials exist, at least within the two species jointly, for the production of the cleistogamous type which would mechanically enforce inbreeding. Cleistogamy as we have observed it could not be a workable inbreeding mechanism, since sudden appearance has precluded its accompaniment by the necessary correlated adjustment. Its complexity of inheritance s, however, such as to leave little doubt about the possibility of it

developing slowly and with increasing efficiency, as would be required if it were to be accompanied and matched by these other adjustments.

These two species of *Antirrhinum*, obligatory and partial cross-breeders though they are respectively, have between them the latent genetical possibility of cleistogamy. In other words crossbreeders can carry, and carry in a realisable form, the latent possibility of inbreeding, just as must indeed be the case if, as has been supposed (Mather 1943*b*, Darlington and Mather, 1949) inbreeding species are constantly evolving from cross-breeding ancestors and as constantly being extinguished by their incapability, due to genetical rigidity, of accommodating themselves to changing circumstances.

6. SUMMARY

A. glutinosum is an obligatory cross-breeder and *A. majus* regularly shows some cross-breeding. In F_2's between these species plants occurred with cleistogamous flowers, such that bees cannot enter and which must therefore set seed by self-pollination. Cleistogamy has not been seen in the parental species nor in the species F_1, though some floral abnormality is found, especially in inbred lines of *A. glutinosum*.

Cleistogamy is variable in expression, some of the variation being non-genetic in origin. The more extreme forms of cleistogamy are regularly associated with an unusual type of vegetative development. Self-pollination regularly occurs in cleistogamous flowers, but is not effective in giving a good set of seed, the cleistogamous plants appearing to have inherited self-incompatibility from *A. glutinosum*. They show little, if any, more true sterility than does *A. glutinosum*.

The inheritance of cleistogamy is complex. Several genes of supplementary effect are apparently necessary for cleistogamous development of the flowers, and others modify the grade (and hence the efficacy) of the cleistogamy which is developed. With such a complexity of inheritance, a gradual change should be possible towards cleistogamy, even though in these experiments it arose suddenly. Cleistogamy is mechanically sufficient to ensure inbreeding, but a successful move towards inbreeding would require simultaneously the abolition of the genetical mechanism which determines incompatibility and also a general re-balancing of the genotype such as would remove, or almost remove, inbreeding depression. The need for this readjustment of genic balance must enforce a gradual rise of any inbreeding mechanism, with which a gradual rebalancing would keep in step. These coordinated adjustments must be regarded not only as necessary, but also as possible in *Antirrhinum*. Thus these species of *Antirrhinum*, cross-breeders though they are, would appear jointly to have already existing within them the genetic materials for the gradual development of inbreeding through cleistogamy. Cleistogamy, which is an established inbreeding mechanism in some

plant species, and indeed inbreeding devices in general, can well be possibilities already latent in the genetical constitutions of cross-breeding species.

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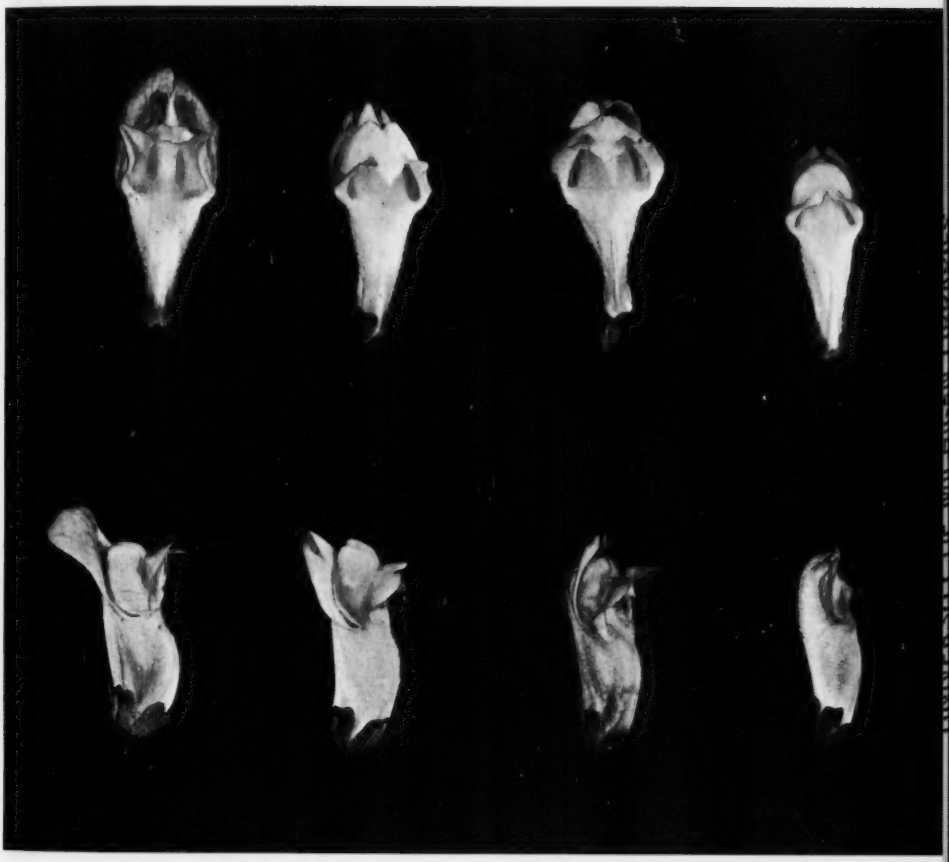
Plate I



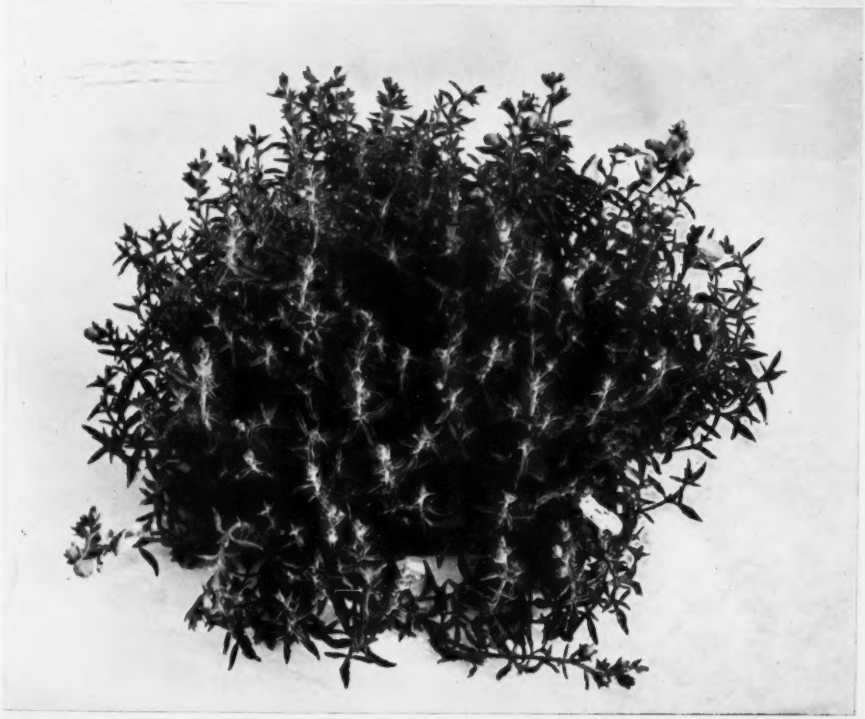
Ventral and lateral views of single flowers of types (left to right) (i) near normal (grade 1), (ii) near normal (grade 2), (iii) partially cleistogamous (grade 3-4), (iv) cleistogamous (grade 5). ×3/2.

Plate II

Normal plants of *A. majus* (above) and *A. glutinosum* (below) to show flower and foliage types. ×1/4.

Plate III

Cleistogamous plants of grade 4 (above) and grade 5 (below). Note the types of flowers and of foliage. Fully cleistogamous plants often show the sparse flowering to be seen in the lower individual. ×1/2.



GENETIC AND SOMATIC ABERRATIONS IN TWO ASYMMETRICALLY MARKED FOWLS FROM SEX-LINKED CROSSES

A. W. GREENWOOD and J. S. S. BLYTH
Poultry Research Centre, King's Buildings, Edinburgh 9

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INTRODUCTION

In the course of an account of an investigation of 7 possible cases of somatic mutation in the guinea-pig, Wright and Eaton (1926) have pointed out that, though many instances of the phenomenon have been observed in *Drosophila*, it is seldom that information about the genetic situation is available in the less frequent reports of its occurrence in vertebrates. That this is still true for birds is clear from the review and discussion by Crew and Munro (1938) of gynandromorphism and lateral asymmetry in this class ; in it their enterprising theory, accommodating all known cases by accounting for slight lateral asymmetry on grounds of chromosome loss, and the larger bilateral differences in size as due to non-disjunction, rests on the absence of contradictory evidence rather than on positive factual support.

The value of these apparent deviations from the known laws of inheritance for further elucidating genetic mechanisms in higher animals, and the comparative rarity of their identification, make it important that experimental evidence concerning them, even if incomplete, should be put on record. It is with this in mind that the breeding records of two visibly abnormal birds of this kind are detailed and discussed in the present paper.

MATERIAL

Both birds were males from the same sex-linked cross, Light Sussex female by Rhode Island Red male, but they arose three years apart and, so far as is known, in unrelated flocks.* As the progeny of this particular cross these males ought to have exhibited the sex-linked epistatic silver plumage of their dams. They ought also to have been heterozygous for yellow/white leg and skin colour and to have manifested the dominant autosomal white. Both showed lateral asymmetry in leg and skin colour, being white on the right side and yellow on the left.

Bird J1.—Bilaterality in plumage colour, silver on the right, red

* We are indebted to Mr R. Scott Miller, Pittachar, Crieff for the first of these birds, while the second was obtained through the kind offices of Miss A. Bowie, West of Scotland Agricultural College Poultry School.

left, was the most striking feature of this bird in which the line of demarcation in both skin and plumage followed the midline of the bird most accurately, even to the tip of the beak (plate I). On neither side was the colour completely pure ; on the silver, *i.e.* " normal " side, odd red feathers occurred and they seemed to increase in frequency with age, though throughout his life this side remained predominantly silver and the irregularities are probably not greater than would be expected in an ordinary male from this cross where silver, though definitely epistatic, is rarely completely so. A certain amount of white on the tips of the red feathers of the " recessive " side was less explicable until the breeder of the bird proffered the information that this appeared to be a hereditary defect which he had occasionally noted in his flock.

Bird J2.—This fowl was also bipartite in colour but the division line was less obvious and there was a tendency for the red to spread beyond the confines of the left to the right or silver side. In particular the dorsal surface of the right wing was mainly red but this may give a false idea of the greater extension of colour since it has its embryological origin close to the mid line. Round the base of the comb there was a cap of purely silver feathers.

In both birds the comb was twisted over to the left or red side, and as it was of the small, stiff, thick variety common to this cross there seemed no reason for this phenomenon other than differential development on the two sides of the body. Both birds had a noticeably larger right wattle but variability as great has been noted in normal purebred Brown Leghorns, where either wattle may be the longer. Their spur lengths were as follows :

J2/Rt. 2·9 cm. Left 3·7 cm. J1/Rt. 5·5 cm. Left 4·2 cm.

While there was nothing obvious in the gait or stance of the birds to suggest that this asymmetry extended to their skeletal structure, it may be noted that both suffered from " bumble foot " and in both it was the left foot that was affected. It was this condition which led to a septicæmia in J1, and the bird was destroyed in poor condition on 20th December 1948 when 5 years old. J2 now in his second year is still alive.

Bird J1.—Post-mortem examination of J1 showed the septicæmia to have been widespread and to have resulted in pathological lesions in practically every organ of the body. Both his testes were inactive ; that on the left weighed 0·52 gm. and on the right 0·80 gm. ; no size difference was discernible between the vasa deferentia. Histologically the spermatic tubules were small, with lumina obliterated by degenerating cells and cell debris ; their germinal lining was scanty and only a few spermatocytes were to be seen. As is usual in quiescent testes there was marked hyperplasia of the interstitial tissue.

Lengths of the main bones of the appendicular skeleton are given in table 1 with those for Crew's (1928) extreme case of lateral

asymmetry from the same cross for comparison. The measurements were made by slide caliper to the nearest millimetre. It is clear that the differences between left and right side are of a small order and

TABLE 1

Bone lengths (in mm.), J1 and Crew's 1928 case

Bone	J1		Crew's case	
	Left side	Right side	Left side	Right side
Humerus	100	*98*	97	*81*
Radius	89	*88*	88	*79·5*
Ulna	99	*97*	107	*88*
Carpo-metacarpus	55	*54*	54	*52*
Femur	114	*114*	107·5	72
Tibia	164	*167*	165	*135·5*
Scapula	96	*97*	94	*88*
Coracoid	75	*73*	75·5	*62*
Total lengths	792	*788*	788	*658*

not consistent in direction ; the right tibia is 3 mm. longer than the left but it is the left coracoid which exceeds its homologue by 2 mm. This results in a net difference between the two sides of only 4 mm. in 790, or about 0·5 per cent. This is smaller than the 2-4 per cent. difference which characterised Crew and Munro's less asymmetrical group. On the other hand, the individual bones appear to show greater variability than was found in a series of normal fowls by Hutt (1929) who reported that in the majority of cases measurements of paired bones were coincident and only in rare cases was a difference greater than 0·5 mm. met with.

Comparison with Crew's (1928) case shows a remarkably close agreement between the length of the bones on the left side of this bird and those of J1, only the ulna and femur showing a noticeable discrepancy.

Since the traceable abnormalities in the two birds related to the exhibition of maternal "dominant" and paternal "recessive" characters (which themselves constituted breed differences in the parents) in one and the same individual, the most obvious course would have been to backcross them to one or both parental breeds. However, a policy of avoiding as far as possible the introduction of strange birds into the Centre's plant (as a disease prevention tactic) led to a different course being pursued, and they were mated to surplus hens from the home-bred Brown Leghorn flock. Like R.I.R. plumage that of the Brown Leghorn is hypostatic to silver. In addition to the first crosses a further generation has been raised from the progeny of J1 by mating some of them (*a*) to Brown Leghorns, and (*b*) among themselves.

While the small number of silver chicks in the first hatch from J1 was sufficient to indicate that he was abnormal germinally as well as somatically, it was not until considerable numbers of progeny had been reared from both males that the full complexity and interrelations in the data collected became apparent.

All the characters examined could not be classified at the same time and thus have not been observed in the same size of sample : this resulted because silver could be identified in the down plumage at hatching but gold—a new segregating colour—could not be distinguished from the paternal-type red until definitive feathers had developed ; it was also at least 6 weeks after hatching before white and yellow leg colour could be satisfactorily differentiated, and sometimes longer when, as often, yellow showed a wide range of intensity. Chicks were sexed when the secondary sex characters allowed, or from examination of the sex glands if they died earlier. As a rule all chicks were examined at hatching and a sample of each group retained for re-examination at 8 weeks or older. Even when the desirability of carrying an unselected sample through to the second stage examination was realised, it was not always possible to do so : birds died, and lack of space or other demands on chick supplies made inroads on many of the hatches.

These variables cause difficulties of interpretation and might make confusing a normal sequential treatment of data leading to integration, so the main results are first set out in the form of a generalised but uncritical summary (table 2) and followed by individual analyses of the various points which require further elucidation and assessment.

Incubation records

J1. Infertility and embryonic mortality in eggs from the mates of the two males show a curious reversal in degree of incidence. For J1 incubations were made for a 3-year period but mainly outside the normal hatching season (in May, June, August and October to January inclusive). Under such conditions fertility was surprisingly good and might have been regarded as a manifestation of hybrid vigour resulting from a three-way cross had not embryonic deaths been rather higher than in purebred Brown Leghorn eggs, incubated at approximately comparable periods. A chi^2 test (percentages weighted for actual numbers) indicated a lack of uniformity in the distribution of dead-in-shell among the hatches (p 1 per cent., df 12) but this was traced to 2 lots, totalling 70 eggs set in October and the beginning of November 1944, in which 30 out of 65 fertile eggs failed to hatch ; their elimination raised the probability of homogeneity to 30 per cent. and brought the mean death rate more in line with that for purebreds. As this is the time of year when spermatogenic activity is at its nadir in fowls, and may cease altogether in individual males, the higher mortality among J1 embryos might be attributable

to some seasonal physiological weakness in the male gamete and need not, *prima facie*, require any out of the ordinary explanation.

TABLE 2

Asymmetrical cocks mated to pure Brown Leghorn hens

	J1	J2	
Eggs set	583	755	
Per cent. Infertility	8·2	30·1	
,, embryonic mortality	21·1	7·15	
,, fertiles hatched	77·0	89·8	
,, hatched of all eggs	70·7	62·8	
Day-old chicks recorded	393	381	
Per cent. males	48·8	45·6	
,, Silvers	5·6	27·0	
Juvenile birds recorded	205*	251	152†
Per cent. Reds	89·0	57·8	60·6
,, Silvers	7·0	30·3	27·6
,, Gold	(3·5)	11·9	11·8
,, White Legs	(6·0	33·1	34·2
,, Silver White/Total White Legs	58	53	
,, Gold White/Total White Legs	(42)	15·7	
,, Red White/Total White Legs	0	31/3	
♂/♀ Silvers	6/15+1	35/66+2	
♂/♀ Gold	2/5	11/19	
♂/♀ White Legs	2/10	31/52	

* From J1, 1 Black "Duckwing" Type male with White Legs unclassified—possibly a silver.

† Restricted sample.

As the condition of the incubating eggs was examined in the normal way by candling (*i.e.* holding over a bright light) it was inevitable that a percentage of very early deaths would be recorded as infertiles, and the low mortality and fertility in the data from J2 at once suggested that an abnormally large number had been so classified. Deaths during the incubation period show a characteristic distribution in the fowl, forming 2 high peaks, one around the 3rd day of incubation and the other from the 18th day to hatching (21 days). If the postulate just made were effective then the mis-classification of non-viable zygotes as infertiles should have resulted in a reduction of early embryonic deaths below the expected numbers. That this was not so is borne out by the actual figures for 41, 3 and 10 embryos died in the 1st, 2nd and 3rd week respectively and this is the exact reverse of the situation deduced.

Reasons for the high infertility must therefore be sought in other directions and it is regrettable that the good results with J1 led to

the view that the labour entailed in pedigreeing the eggs from the individual mates of this one was unnecessary, for it has left open the possibility that though a most vigorous bird, he was showing preference for particular mates and leaving a number of other hens unfertilised.* The only other points which can be made here are that the incubations were carried out between February and June, a time when the best hatching records are to be expected, and that the percentage of infertility showed no undue variation among the different hatches : a chi^2 test yielded a probability of homogeneity over 30 per cent., *df* 13.

External characters.—Despite the wealth of experimental data on the inheritance of morphological characters in the fowl, Jull's (1940) review reveals that though there is a good deal of loose information about the behaviour of isolated pairs of traits there is far from a sufficiency of integrated evidence about the genetic constitution of various breeds on which to predict segregations from particular crosses. In regard to the three breeds concerned in the cross under consideration, Light Sussex, R.I.R., and Brown Leghorn, the only sound lead available is that the silver plumage of the Light Sussex behaves as a sex-linked dominant unit in relation to the other two types. This difference is distinct in so far as it relates to silver and non-silver but takes no account of the intra-class variation which is considerable in the present case. Neither Brown Leghorn nor R.I.R. plumage types appears to be allelic to silver so that the sex-linked effect rests on epistasis and this favours the segregation of hidden colours or pattern in the triple cross.

Actually the variation encountered could be regarded mainly as different degrees of modification of the parental types and in only one case has it been necessary to recognise an additional class, gold, for our present purposes. It may also be noted that indication of Brown Leghorn ancestry are traceable in the feathering of most non-silvers and takes the form of an imposition of Brown Leghorn pattern on the ground colour of other types with all degrees of effectiveness, from that giving a mismarked R.I.R. plumage at one end of the scale to that giving a mismarked Brown Leghorn type at the other ; in the silver class is showed its influence in the appearance of " duckwing " patterns, and their female homologues but only in a proportion of cases.

As already mentioned it was noticeable at hatching that the number of silver-plumaged progeny of J1 was far below the expected ratio of 50 per cent. though they appeared in all but one of the settings in numbers varying from one to three ; it was not until the birds were several weeks old that a like shortage of white-legged individuals was evident. At first it appeared that white legs were restricted to

* Recent matings of J2 to trap-nested hens have indicated that his low fertility is due to infrequent matings : females show periods of infertility interspersed with sequences of fertile eggs.

the silver group but then they turned up in rare non-silver birds ; these were much paler than the average of the group and have been designated *gold* in opposition to the more definite shades of *red* though there was no clear cut demarcation between them. In respect of the data from the first male alone the decision to regard them as separate classes was open to considerable doubt and it might have been argued that the genes regulating leg colour were having a diluting effect on plumage colour for only a single gold bird with yellow legs was identified. The postulate had the advantage, however, of rationalising the relation found between leg colour and plumage : about half the white-legged birds were gold and half silver and there were 7 silver white and 7 silver yellows. The lack of a similar relation between gold whites and gold yellows is accounted for by lack of ability to identify the latter class. Despite their numerical weakness such classes were strongly suggestive of the idea that they derived from a small part of the germinal tissue which, apart from the absence of red, was behaving normally and producing gametes in the 1 : 1 ratio expected from monohybrid heterozygotes ; the remainder of the testes was then defective in that it carried neither the genes for white legs nor for silver.

When descriptions of J2's progeny became available it was seen that the same groups were again segregating but that there was an additional class—red plumage with white legs. Though still below the expected value of 50 per cent. the frequency of silver is much greater here, yet again approximately half the silver birds were white-legged and half the white-legged ones were silvers.

It is of some importance to decide how reliable the size classes are here : the figure of 27 per cent. obtained for the silvers at hatching might be taken as indicating a parameter of 25 per cent. which would accord with a postulate that one testis was producing silver gametes in the normal ratio while the other lacked the gene entirely. At the second examination the proportion had risen to 30 per cent. indicating that discrimination, artificial or otherwise, against non-silvers had operated between the two dates. If this fell mainly upon gold, as it might by chance or through differential viability it could markedly affect the size of the group. The only check on this is to compare the frequency of the segregating classes in the more complete groups (152 chicks) with that for all. Table 2 (restricted sample) shows that this is practically without effect on the percentage of golds, and though the silvers return to a value approaching that in the day-old ratio, it is the reds, not the golds which profit from their loss.

From the analyses of the second stage examination (table 3) it can be seen that silver white, silver yellow, and red-plus-gold white constitute classes of approximately equal size but that red-plus-gold yellow is about three times as large. This suggests that the gonadal situation is similar to that in the first half-sider in that there is again one part of the germinal tissue which is deficient as to silver and white

(responsible for the excess in the red-plus-gold yellow class) and another which is behaving more or less according to expectation ; it is in fact behaving more normally than in the first cock for, since

TABLE 3

J2 progeny. Second examination

Silver White	Gold White	Red White	Silver Yellow	Gold Yellow	Red Yellow	Total
♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀
16 28	3 10	12 14	12 20	8 9	57 62	108 143
	♂ ♀			♂ ♀		
	15 24			65 71		
44	39		32	136		251
♂♂/Class						
36·4 per cent.	28·5 per cent.		37·5 per cent.	47·8 per cent.		43·0 per cent.

Note.—Though ignorant of the exact situation, particularly in regard to dominance and allelism in some of the characters examined in the crosses, it may aid in understanding the interpretation put upon the segregations listed above and in table 6 if the matings are represented by simple genetic formulæ which can accommodate the results without prejudice to these gaps in our knowledge. The letters S and W are in common usage as symbols for the sex-linked gene producing silver plumage and the autosomal one for white skin and leg colour respectively. In addition, for the present purpose, R may represent R.I.R. plumage colour and B, the Brown Leghorn type ; the corresponding small letters denote the absence of the genes causing these manifestations, but with one addition : while r represents the absence of the basis of R.I.R. colour in the Brown Leghorn, let ρ indicate its absence in the presence of Light Sussex colour genes. The " genes " presumed to come from the sire are above the line in each individual's formula, those from the dam, below. No linkage is inferred.

On this basis the cross between J2 and Brown Leghorn females would be :—

$$\frac{sRbw}{S\rho bW} \times \frac{srBw}{-rBw}$$ and their male progeny should have included

Reds : $\frac{sRbw}{srBw}$ or $\frac{sRbW}{srBw}$

Golds : $\frac{s\rho bw}{srBw}$ or $\frac{s\rho bW}{srBw}$

Silvers : $\frac{S\rho bw}{srBw}$ $\frac{S\rho bW}{srBw}$ $\frac{SRbw}{srBw}$ or $\frac{SRbW}{srBw}$

The female progeny should comprise the same groups but in each case with the lower s missing.

silver and red are non-allelic, the heterozygote mated to the Brown Leghorn should yield two classes in the recessive half of its progeny, R.I.R. red and its allele or complementary group from Light Sussex or Leghorn.

On a unit basis of inheritance then, the number of golds does not fall far below expectation for the two classes should be the same, and together equal that for silvers. Further evidence in support of this was actually available from the latter though exact data are lacking

as its significance was not at first realised. Two main classes were recognised among the silvers—" self " and " duckwing." The amount of non-silver in the latter varied a good deal and closer inspection revealed that it was possible to split the class into those in which the colour on the back and wing was the red-gold hue of the Brown Leghorn and others in which it was the darker, flatter colour of the R.I.R. Presumably a similar genetic dichotomy was present in the self silvers but could not be expressed. Thus, on the assumption that one testis was normal, we might expect the progeny from it to segregate in four groups each accounting for 12·5 per cent. of the cock's total offspring, silver non-red, silver plus red, non-silver non-red (*i.e.* gold), and non-silver plus red. Since all the chicks from the other testis would fall into the latter category, the distinguishable classes expected would be 25 per cent. silvers, 12·5 per cent. golds and 62·5 per cent. reds which is very close to the actual proportions obtained.

Sex ratios.—A notable feature of table 3 which has not yet been mentioned is the shortage of males in three of the four main classes and the consistency of this phenomenon in both cocks' offspring must now be examined. With a figure of 48·8 per cent. males there seemed nothing remarkable about the sex ratio of chicks from J1, and the preponderance of females in the rare gold and silver plumage, and white-legged, classes could be regarded as a chance result of small numbers until the same bias was found in the data from J2 for these groups. The substantiation or refutation of this phenomenon is of some import, for in birds the male is the homogametic sex and does not normally control determination of sex in his offspring. Though the three affected classes in table 3 are very alike in their proportion of males, they are again suspect because of the incomplete hatching groups, but use can be made of the fact that silvers are identifiable at hatching to obtain ratios for nearly complete samples at that date (table 4). This actually enhances the shortage of silver males but unexpectedly gives a non-silver group in which the sexes are nearly equal. Whatever the situation in the latter it is difficult to avoid the conclusion that the silvers are abnormally distributed as to sex. Among the separate hatches only two show an excess of males (each 4 ♂♂ 3 ♀♀) and when they are grouped as indicated in the table to form samples of a more uniform total size (56-69) the trend is even more convincing : the six silver groups so obtained have an average of 5·83 ♂♂ and 11·0 ♀♀, giving a mean difference of 5·17 birds with a standard error of 1·47 ; in the larger non-silver group the comparable mean difference is $0{\cdot}67 \pm 2{\cdot}43$.

For both classifications there has been a differential wastage of the sexes between the two examinations. It might have come about through natural causes, expressed in mortality, or artificially through culling of more males. These sources of loss are analysed in table 5 : equal numbers of silvers were disposed of, but 13 ♀♀ and only 1 ♂ are recorded as having died. Among the non-silvers the sexes died

in equal numbers but 37 ♂♂ and 25 ♀♀ were culled; their inequality at the second examination is, therefore, due to chance in culling; since this was not consciously based on health traits, there are no

TABLE 4

J2 progeny. First examination

Hatched	Silvers			Total				Non-Silvers		
	♂	♀	Not sexed	♂	♀	Not sexed		♂	♀	Not sexed
7.2.49	...	2	...	4	2		64	4	...	...
2.5.49	4	10	...	28	30			24	20	...
9.5.49	4	3	...	26	21		69	22	18	...
16.5.49	...	4	...	9	12	1		9	8	1
23.5.49	4	7	...	18	22		63	14	15	...
30.5.49	3	6	1	9	12	2		6	6	1
6.6.49	4	14	1	18	33	5	56	14	19	4
13.6.49	6	10	...	26	37	4	67	20	27	4
20.6.49	6	7	...	20	21		62	14	14	...
27.6.49	4	3	...	9	12			5	9	...
	35	66	2	167	202	12	381	132	136	10
♂♂/Class . .	34·65 per cent.			45·26 per cent.				49·25 per cent.		
Av. for grouping	5·83♂♂ 11·0 ♀♀							22 ♂♂ 22·67 ♀♀		
Difference . .	5·17±1·47 (S.E.)							0·67±2·43		

TABLE 5

Source of Loss between first and second examination

	Silver		Gold		Red		Gold+Red		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Second examination .	28	48	11	19	69	76	80	95	108	143
Died . . .	1	13+2	?		?		15	16+9	16	29+11
Culled . . .	6	5	?		?		37	25+1	43	30+1
First examination .	35	66+2	?		?		132	136+10	167	202+12

observational grounds to support the idea of an abnormal sex ratio here. If, however, the postulate still remained open on other premises it may be noted that there are three possible ways in which the phenomenon might operate: it might be affecting (*a*) the golds alone, (*b*) the white-legged non-silvers, or (*c*) the entire group postulated to be homologous to the silver one. In the present sample, either of the first two conditions could occur without causing more

bias than there is in the non-silver group at hatching, but in the third case a contrary, compensatory ratio in the remainder of the red, yellow-legged birds would be necessary to achieve this.

Backcrosses of J1.—Breeding from the progeny of J1 served firstly in the search for any peculiarities he might have passed on, and secondly to check how the observed traits were being inherited. Nothing unaccountable was observed in their breeding behaviour, or in the appearance of the small groups of offspring raised from each mating. Out of 461 chicks hatched from the various tests, 204 were males and 44 unsexed. If there was any tendency to an excess of females it was in the crosses of 5 red F_1 hens with a Brown Leghorn and later a gold cock (39 ♂♂ : 49 ♀♀+6) but this bias appeared non-significant when 11 ♂♂, 18♀♀ and 5 unsexed chicks, the progeny of one dam, were excluded.

The crosses made and the situation found with regard to plumage and leg colour are summarised in table 6. The females used were F_1 from the mating of J1 with Brown Leghorn hens except for four golds indicated in the table ; these were two pairs of progeny of a Brown Leghorn cock mated to a silver and a gold hen respectively. The males used were a purebred Brown Leghorn, an F_1 silver, and F_1 gold, and an F_1 red Brown Leghorn type cock ; no progeny from the last bird were available for a second examination so data from it are based on day-olds. In all F_1 matings the Brown Leghorn genotype should be present in the heterozygous state in each side of the cross. In the backcross F_1 to Brown Leghorn male there are three gametic complements of Brown Leghorn genes available for segregation in the progeny, and with the few gold hens from this cross, used in further tests, there may be theoretically up to the same maximum.

The summarised test matings for white and yellow leg colour accord well with a monohybrid ratio ; the slight excess of yellows in the backcross is due to the higher proportion from two of the three red females mated to a gold cock (4 : 7 and 3 : 9) but the third red dam produced 8 white and 8 yellow-legged offspring.

Silver plumage when taken in apposition to the absence of silver in the other three groupings behaves as a sex-linked unit dominant to them all. Gold also can be regarded as a simple dominant to Brown Leghorn type (though the pattern of the latter is present to varying degrees) but the evidence as to the relations of red and gold, and red and Brown Leghorn is not conclusive. Inherited on a simple basis, if gold were dominant to red, but non-allelic, the expected classes from mating their F_1 representatives would be 2 gold : 1 red : 1 not red or gold, but if the situation were reversed the ratio would be 2 red : 1 gold : 1 not red or gold. The results appear to be in better agreement with the second postulate. If this were so, whether gold were carried by the red birds or not, the appearance of red, gold, and Brown Leghorn individuals as progeny of this cross is according to expectation. Gold carried by the red F_1 birds however, would be

expected to segregate out when they were crossed with Brown Leghorns, but there it has not been identified.

We are thus left with the suggestion that red is dominant to gold, and incompletely so to Brown Leghorn pigmentation. In the reds tested it does not appear likely that gold is present, nor is there any evidence that silvers were carrying red, for this colour did not appear

TABLE 6

F1 backcross progeny

PLUMAGE

Sire	Dam	Progeny: Sex ratio ♂	♀	Plumage	Main ratio expected
Pure Br. L.	×Silver	5	9	5 Silver 9 non-Silver (3 Gold 6 Br. L.)	7 : 7
	×Gold	22	25	23 Gold 24 non-Gold (all Br. L.)	23·5 : 23·5
	×Red	12	12	9 Red 15 non-Red (all Br. L.)	12 : 12
Red Br. L. F_1*	×Silver	7	5	7 Silver 5 non-Silver	6 · 6
	×Gold	11	14	... Silver 25 non-Silver	: 25
Gold F_1	×Silver	9	7	9 Silver 7 non-Silver (5 Gold 2 Br. L.)	8 : 8
	×Gold†	5	5	9 Gold 1 non-Gold (Br. L.)	7·5 : 2·5
	×Red	18	21	20 Red 19 non-Red (12 Gold 6 Br. L. 1 Buff)	19·5 : 19·5
Silver Backcross	×Silver	18	19	29 Silver 8 non-Silver (4 Gold 4 Br. L.)	28 : 9
	×Gold	13	19+1	16 Silver 17 non-Silver (11 Gold 6 Br. L.)	16·5 : 16·5

LEG COLOUR

Parents	Progeny: Observed	Expected
	White Yellow	White Yellow
White F_1 × White F_1 .	49 : 15	48 : 16
White F_1 × Yellow . .	60 : 70	65 : 65
Yellow × Yellow . .	... : 24	... : 24

* Day-old ratios only.

† Four Backcross females from Br. L. × Silver and Br. L. × Gold Matings.

in the progeny of any of the 3 silver hens and cock tested. Hutt (1949) considers that all birds are basically either silver or gold and that the two colours are sex-linked and allelic. In the present case gold has shown no indication of sex linkage and though there was ample opportunity in the gold female × Brown Leghorn male matings the plumage types showed no abnormality of distribution in relation to sex. Its behaviour thus is more in line with the gold described by Punnett (1948) which he concluded to be autosomal.

DISCUSSION

The similarity in the expression of the somatic and germinal abnormalities in both J1 and J2 suggests they have a common origin very early in ontogeny and prior to the migration of the presumptive primordial germ cells into the embryonic gonads.

Since in J1 the external manifestation was bilateral, and in J2 roughly so, the irregularity could not have taken place later than the

TABLE 6 (*continued*)

Possible formulæ for the plumage of sires and dams used
(see table 3 for explanation of symbols)

Sire		Dams	
Pure Br. L.	$\frac{srB}{srB}$	Silver	$\frac{S\rho b}{-rB}$ or $\left(\frac{SRb}{-rB}\right)$
		Gold	$\frac{s\rho b}{-rB}$
		Red	$\frac{sRb}{-rB}$
Red Br. L. F_1	$\frac{sRb}{srB}$	Silver	$\frac{S\rho b}{-rB}$ or $\left(\frac{SRb}{-rB}\right)$
		Gold	$\frac{s\rho b}{-rB}$
Gold F_1	$\frac{s\rho b}{srB}$	Silver	$\frac{S\rho b}{-rB}$ or $\left(\frac{SRb}{-rB}\right)$
		Gold Backcross	$\frac{srB}{-\rho b}$ or $\frac{srB}{-\rho B}$
		Red	$\frac{sRb}{-rB}$
Silver Backcross	$\frac{srB}{S\rho B}$, $\frac{srB}{SrB}$, $\frac{srB}{S\rho b}$	Silver	$\frac{S\rho b}{-rB}$ or $\left(\frac{SRb}{-rB}\right)$
	$\frac{srB}{Srb}$, $\left(\frac{srB}{SRB}\right)$ or $\left(\frac{srB}{SRb}\right)$	Gold	$\frac{s\rho b}{-rB}$

The indications are that the bracketed genotypes did not occur in the progeny of J1.

early cleavage divisions which determine the axial organisation of the embryo. It could even have occurred at the first cleavage division, for irregularities of bilaterality of the type noted in the plumage of J2 are not inconsistent with development from a gastrula in which the two halves differ genetically : the complete cap of silver feathers lies near enough to the midline to be accidentally symmetrical, and the wing bud also has its origin close to the plane of symmetry, so that only a very slight overgrowth of the red side would be required to produce a wholly red wing. As close an association with the two sides of the body would not be expected in the germinal tissue for its precursors, the primordial germ cells, are believed to have their origin external to the gonads and to reach them by amœboid movement through the forming embryonic blood vessels (Willier, 1937).

This is as far back as the phenomenon can be postulated however, in one bird at least, for the data reported present a bar to the idea that it could have had its origin in the zygote itself. If, for example, polyspermy had resulted in double fertilisation, the Light Sussex ovum nucleus might have fused with a sperm to produce the expected heterozygous constitution in the cells of one part of the organism, while the remaining part developed from purely R.I.R. chromosomes. There is nothing in the breeding behaviour of J2 in disagreement with this but the hypothesis infers that both red plumage and yellow leg colour should be carried by the normal (silver) part of the gonad so that the absence of red, white-legged, birds among the progeny of J1 would require explanation. This might be a matter of chance : only 22 silvers were identified at hatching and the non-silver group should be about the same magnitude, with half the birds white-legged. As 5 of the 7 golds recorded had white legs this leaves only another 5 or 6 unaccounted for which could have been red or gold. Thus it is not impossible for the absence of this class to be due to chance in sampling, particularly as leg colour could not be determined until the second examination.

There is a further check on the situation in that half the F_1 silvers ought also to carry red : only 4 silvers have been adequately tested genetically and none threw reds : this assumes a simple mode of inheritance of red but for present purposes this seems justified by the backcross matings reported in table 6. There, too, it may be noted there were 24 non-silver offspring with an F_1 silver parent, in any of which red would have been visible if present but only golds and Brown Leghorns are recorded.

Phenotypically also the evidence from the first cross silvers is against the presence of red : among the progeny of J1 there are two types of silver males, self colour with black points and " duckwing," with less clearly differentiated female homologues. The latter pattern carried a red bar on the wing but it was the bright red of the Brown Leghorn plumage and not the dark chestnut typical of the R.I.R. On the other hand there was the group of J2 silver offspring of both sexes, which showed clear evidence of their Rhode Island inheritance : most of their dorsal plumage was dark chestnut and gave the impression of R.I.R. birds with a silver Columbian pattern superimposed (see p. 223). Finally, though less reliably, the mismarked feathers on the silver side of J1 himself appeared to be of a lighter shade than the plumage of the other, while the red feathers on the two sides of J2 seemed more alike.

Thus, though nowhere conclusive, all the evidence seems to point in the same direction, namely, to the absence of red in the silver part of the germinal tissue of J1 and so to the conclusion that he is not the product of double fertilisation. In J2 on the other hand, the findings with regard to plumage and leg colour support such a theory of his origin, yet the abnormalities exhibited by the

two cocks are of so similar a character as to call for a similar explanation.

An alternative zygotic irregularity where female gamete and polar body united to form one of the first pair of cells and sperm formed, the other is still more unlikely since by itself it fails to account for silvers with yellow legs or red with white. Both mutation and non-disjunction seem out of the question with the number of independently segregating characters observed to be disarranged. As a possible cause, simple chromosome loss suffers the same disadvantage as double fertilisation in that it requires the loss of two independent genes on the red side of both birds plus the loss of the red from the silver side of J1. Also as a sex-linked gene, silver, is involved ; sex or size differences of observable magnitude might have been expected in the two sides of both birds.

The suggestion that there is some incompatability between the gametes of the two breeds, which leads to repulsion between the two chromosome sets introduced into the zygote, is attractive, the more so since this particular cross accounts for more (five) of the previously known cases of lateral asymmetry in the fowl than any other breed or cross (Crew and Munro, 1938). There may be, however, less germane reasons for this : whatever the cause of the phenomenon, it is clear that it can only express itself in the presence of heterozygous alleles, or epi- and hypostatic genes, capable of segregating in an observable form. Commercial crosses with well-marked breed differences should provide suitable ground for its appearance. Most of the 14 cases reviewed by Crew and Munro were of such an origin and only two could be regarded with any certainty as purebred ; four showed lateral differences in plumage colour but none of these were Light Sussex × R.I.R. cross, and 11 yielded segregations of shank characters. Abnormalities of the latter class may occur more frequently than plumage ones, or it may be that they are more obvious despite the attention automatically drawn to feathering in sex-linked crosses by its use as a criterion of sex. It must be rare for plumage differences to be so perfectly bilateral as they were in J1, and birds apparently marked erratically would be less likely to attract attention. Thus it is improbable that J2 would have been picked up but for the sender's knowledge of the first mosaic cock ; the breeder of J1 has also stated that he had noticed other but less well-marked cases of the condition in his flock. Similar predisposing causes may have operated in the detection of most of the other 5 cases from Light Sussex × R.I.R. matings for after Crew (1928) had published a description of the first one all the others were brought to his notice at later dates. Thus the high number of specimens of lateral asymmetry from this particular cross is not in itself sufficient proof of its higher frequency here. The position then appears to be that none of the more straightforward explanations satisfy the conditions which appear to exist in J1 while all, with varying degrees of probability, might be capable of

accommodating the data from J2. Silver and white legs show no indication of linkage ; mutation, translocation, or non-disjunction, would therefore each involve two distinct steps. In a sense this might also apply to chromosome loss but on the other hand it could be regarded as the single act of dropping anything from two to a haploid set of chromosomes. In this respect it would approach the situation expected with double fertilisation where a second sperm is assumed to undergo development in the cytoplasm of the completed zygote : unless there was a reversion to the diploid condition through some atypical cleavage of the kind that has been reported in frogs (Parmenter, 1940) both would result in the presence of unequal numbers of chromosomes on the two sides of the body. The conclusions of Hutt (1929) and Crew and Munro (1938) suggest that this should be accompanied by lateral size differences, and Fischberg's (1948) work gives actual evidence of such distortions in *Triton alpestris*, but they have not been observed in the present birds.

Again the condition of haploidy, if it could develop in half the body to the extent of sperm formation, would be difficult to identify except by cytological means. It must be inferred, however, that the spermatogonia producing red plumage are either haploid or homozygous for red since otherwise, a much greater proportion of other colours would have been expected among the progeny of both mosaic cocks. In the case of J1 an irregular " reduction " division could have resulted in leaving red in one cell and silver in the other but raises the problem of why yellow legs occur with both red and silver and white legs only with silver.

SUMMARY

Two F_1 cocks, products of mating Light Sussex females to R.I.R. males, each exhibited the plumage and leg colour of *both* parents ; in one the colour distribution was almost perfectly bilateral, in the other less so.

In both cases the abnormalities extended to the germinal as well as the somatic tissue. Breeding tests with the second cock suggested that he had one normal testis while the other was producing no sperm which carried the genes for silver plumage or white legs.

With the cock showing the more perfect bilateral asymmetry the situation was similar but the proportion of silver chicks produced was much smaller, and it seemed likely that the " silver " portion of his testis also was deficient and lacked the genetic basis for R.I.R. type plumage. The breeding behaviour of his progeny was normal.

No theory of the origin of the phenomenon could be formulated which would accommodate the data from both cases.

"J1" ♂

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THE HISTORY OF THE GARDEN HYACINTHS

C. D. DARLINGTON, J. B. HAIR and R. HURCOMBE
John Innes Horticultural Institution, Bayfordbury, Hertford, Herts

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1. ORIGINS

THE origin of the garden hyacinth is simple enough, and its improvement recent enough, for us to describe its history more accurately than that of most garden plants. Krelage in his recent account is able to refer not only to the illustrations but to the actual varieties raised during the last three hundred years as a record of the achievements of successive generations of hyacinth breeders.

Hyacinthus orientalis has been collected during the last thirty years. We have seen specimens flowering in the gardens of Mr E. A. Bowles (from Palestine), Major A. Pam (from Syria) and Colonel F. C. Stern (from the Taurus Mountains). With their spikes of half a dozen pale blue flowers they agree with the figures and descriptions of Dodoens, Clusius, Besler, L'Obel, Sweerts and Parkinson between 1562 and 1640. In this period, just after its introduction from Turkey, there was little change beyond the appearance of white and pink and double mutants or segregates, and of larger spikes. Then came a great advance. Van Kampin's catalogue of 1739 lists nearly 400 varieties of hyacinths—300 double. In 1752 Guyot writes (according to Zirkle) : " Hyacinths are all either blue or white ; some have a little rose colour. . . . Yellow hyacinths will never be produced."

Before 1768 lilac and yellow colours had appeared. Dutch breeders had raised the 1670 varieties numbered and named at that time in the great treatise of the Marquis de Saint Simon. And they had raised many more which had failed to survive. Since that time another three thousand or more have been raised and named,

recombining the pigment mutations. Of all these only a hundred or so survive. The need for denser and denser spikes for show led first to the selection of double flowers. This was succeeded by a selection of fasciated spikes which give the same dense effect with earlier flowering and a more rapidly propagating bulb. These tendencies were noted in the *Gardeners' Chronicle* of 22nd March 1862 and 3rd April 1886. Now, few double varieties are found in commerce and none of them of the flamboyant monstrosity of former times.

The direction of yet a third change is indicated by Shirley Hibberd (1880) who says, that in 1873 he had flowered some 500 of the surviving varieties. "Blue and white varieties were in most cases superior in quality to the red. Thus it appears that in raising flowers by cross breeding we must expect to lose quality with every gain in departure from the normal type." We have fancy colours, he considers, at the price of a loss of vigour.

In all this history there is no evidence of hybridisation. The garden hyacinth is derived like the sweet pea from a single, not very variable, wild ancestor. The chromosome complement bears out this conclusion : for the whole range of varieties the forms of the chromosomes are, as we shall see, almost invariable and they do not occur in the only other species of the genus, *Hyacinthus amethystinus* ($2n = 28$: Darlington, 1933).

2. VARIETIES, SPORTS AND NAMES

New hyacinth varieties have been chiefly raised from seed and named by the breeder when introduced. These varieties produce bud sports, *i.e.* somatic mutations, especially for colour and doubleness, but perhaps also for quantitative characters such as vigour. Most supposed mutations are lighter in colour than the parent and dark blue varieties seem to give most mutants. They are of the kind expected of genuine somatic mutations, recessives being commoner from dominants than the reverse. To these mutants, entirely new names may be given and the result is then straightforward, as we shall show in our tables. Thus the double mutant of *L' Innocence* is named *Madame Sophie*. But the result is not straightforward in two other situations.

In the first place, new names have often not been given. Thus Kersten (1889) says that there are three *Queen of the Blues*—from Haarlem, Overveen, and Hillegom. Also *Grand Vainqueur* was known in 1874 in white, yellow, and pink forms, both single and double. Again there are single and double forms of *La Grandesse*, the single being the one we have studied.

In the second place, new names are sometimes given when no obvious mutation has occurred. The same variety is then known under synonyms, *e.g.* :—

Maria Catherina = *Robert Steiger*; *Salmonetta* = *Orange Boven*; *Mme. du Barry* = *Scarlet O'Hara of Blom* = *Tubergen's Scarlet*; *Bismarck* = *Blue Queen*; *Queen o' Whites* = *Blom's Gem*

Our chromosome studies suggest other pairs as candidates for synonymy, such as :—

Pink Perfection = *Princess Margaret*; *Dr Stresemann* = *Winston Churchill*

A third special difficulty has arisen through the sale of immature bulbs as " miniature " hyacinths for bedding and forcing. For these Messrs Sutton's, in 1920, adopted the name of *Cynthella* hyacinths. The flowers being smaller and the spikes looser than those of the mature variety, the trade did not like to give them the same varietal names as the mature forms and a whole series of sprightly new names were invented for them such as *Minnie* and *Maggie* and *Fair Annie*. Owing to the disappearance from cultivation of many varieties in their mature form, we have had to resort to these Cynthellas and we have marked them (C). We have tried to make out their synonymy with the help of the chromosome identity so far as we could, *e.g.* :—

Schotel = *Fair Ellen* (C); *City of Haarlem* = *Morning Star* (C); *Queen o' Whites* = *The Bride* (C); *Nimrod* = *Cinderella* (C)

3. CHROMOSOMES OF THE VARIETIES

(i) *The complement*

The importance of the hyacinth for us depends on the variations in its chromosome complement which the living records of its evolution are still capable of displaying. We can record the achievements of the plant breeder in each period, not only by the forms produced but by the chromosomes determining these forms. Moreover, in its chromosome structure this plant is uniquely favourable for such an inquiry.

The hyacinth has five distinct chromosome types which vary in number independently (within limits which we shall examine) in the improved varieties so that scores—or perhaps hundreds—of different chromosome combinations can be recognised under the microscope. The haploid chromosome set of eight may be represented, after slight shortening with pre-treatment and Feulgen staining, as follows :—

L—17 μ	L—20 μ	M—9 μ	S_1—5 μ
L—19 μ	L^n—20 μ nucleolar	M—9 μ	S_2—5 μ

The sub-types of L's and S's cannot be told apart in every cell. They have not, therefore, been recorded for individual pollen grains and, only in our later work, for individual varieties.

Yet another, but less certain, distinction concerns the width of the nucleolar constriction. In one of the four L^n chromosomes in

Myosotis, *L' Innocence* and its mutant *Mme. Sophie* it seems to be weaker than in the other three which are normal.

Previous workers had counted and classified the complements of 46 varieties (seedlings and somatic mutants). We have dealt with another 61. The total of 107 are recorded for the chromosomes in relation to their dates and modes of origin, and colours, in table 1.

(ii) *Sports, new chromosomes and corrections*

All undoubted bud sports proved to have the same chromosome numbers as their parent varieties, with one exception, *Queen of the Whites* has an S_2 chromosome in place of an S_1 found in *Queen of the Blues*: $4\,S_1+2\,S_2$ has become $3\,S_1+3\,S_2$, this implies two changes but it is not so improbable as it seems since both changes involve a movement towards normal balance.

Three varieties, one a bud sport, have new chromosome types, as follows :—

(i) *Madame du Barry*, introduced in 1920, arose as a sport from the normal diploid variety *Distinction*. It has a deficiency amounting to two-thirds of one arm of an L chromosome and has lighter red flowers than its bud-parent. The loss of the segment has apparently revealed a recessive colour character. Such a deficiency-heterozygote arising somatically is unique among diploid organisms (fig. 1A). A reciprocal change was found in the parent variety (plate I, fig. 1).

(ii) *Fireball*, another red variety, arose in 1867 as a seedling. It is a triploid but has a translocation from L to S_2 (or an interchange between them) giving two new types of chromosomes (fig. 1B).

(iii) *Grace Darling* is a bogus *Cynthella* name and not a period name. We do not know its genuine synonym among the old varieties. It has one M chromosome with a subterminal centromere, *i.e.* deficient in the short arm.

Two losses and one interchange thus represent the sum of observable structural changes that have arisen in the hyacinths in nearly 400 years' cultivation. In the beginning, before the differentiation of the varieties, the chromosome uniformity must have been even greater.

The chromosome studies enable us, while confirming the documentary evidence of origin for some varieties, to contradict it for others. The evidence must be weighed in each case, as follows :—

(i) *Mr Dames*, the only pink variety with a high chromosome number, is said by some connoisseurs to be a cross between a pink mutant (*Etta*) of *Lord Balfour* and *La Victoire* both normal diploids. The origin of a near tetraploid at one step from two diploids is unlikely and is doubtless the usual breeders' guess. An alternative guess is *Jacquis* × *Amiral Courbet*: this we cannot test since the two parents are of unknown number.

(ii) *Cardinal Wiseman* is said to have given rise to *Marconi* as a bud sport. If the counts and names are right it has, therefore, lost three

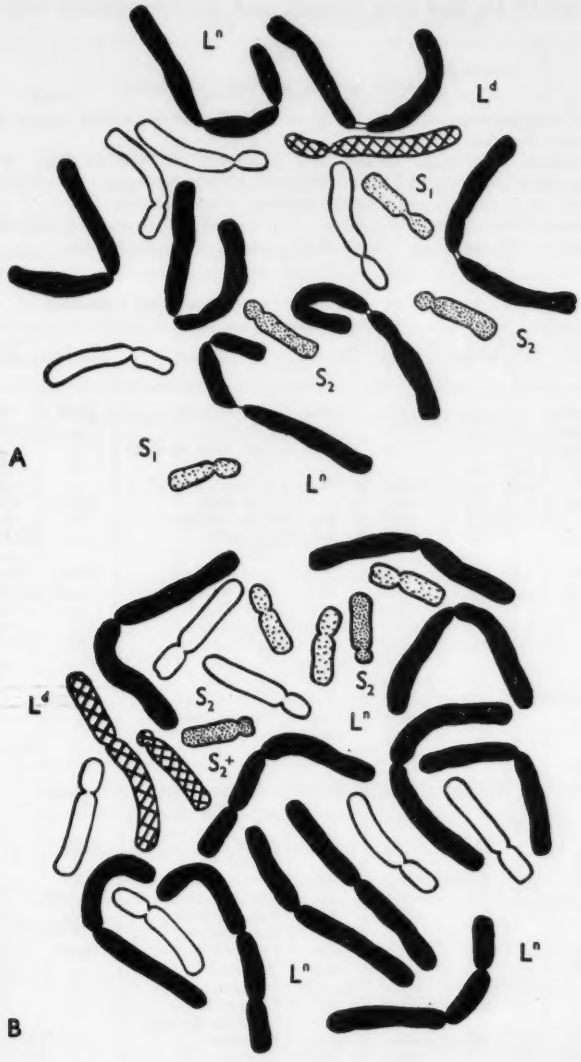

FIG. 1.—Complements of varieties with aberrant chromosomes.

A. *Madame du Barry* with a deficient L^d arose as a bud sport from the normal diploid *Distinction*.

B. *Fireball*, a triploid variety with an interchange, giving a short L^d and a long S_2+. ×2000.

chromosomes and become balanced. The count, however, was an early one by De Mol from sections, and the complement very unusual

TABLE 1

Hyacinth varieties classified (107 *forms*)

L, M and S chromosome numbers are given according to the author named, and L^n and S_2 sub-classes where recorded.

D = Darlington, 1926, 1929. D and M = Darlington and Mather, 1944. S = Stow 1930. Hair = Hair unpub. M = de Mol, 1921. RH = R. Hurcombe unpub. U = Upcott, 1937.

All varieties are seedlings except those labelled *mut.*, somatic mutant.

Dates of introduction chiefly from Krelage, 1947 : usually 25 years after sowing seed.

B, blue flower ; BB, dark blue. (C) Cynthella name. (d) double flowers.

A. Diploids : 8L+4M+4S = 16 (35 varieties, 1 mutant)

Name	Author	Date	Colour	Name	Author	Date	Colour
Romaine Blanche	M	1580	white	*Mauve Queen*	Hair	1875	mauve
L'Amie du Cœur	,,	1820	pink	*Distinction*	,,	1880	red
Maria Catherina	,,	1830	red	mut. *Mme. du Barry*	,,	(1920)	pink
Homerus	,,	1840	,,	*M. o. Lorne*	M	1881	yellow
B. van Tuyll	,,	1841	pink	*Yellow Hammer* *	,,	1883	yellow
Prol. monstrosa	,,	1844	...	*Zulu King*	Hair	1890 ?	BB
Othello	,,	1848	BB	*King Haakon*	M	1900	?
Gertrude *	,,	1850	red	*Daylight*	,,	1893	salmon
Veronica	,,	1854	,,	*Flora*	,,	1900	?
Gen. Pélissier	,,	1855	,,	*Lord Balfour* †	Hair	1900	BB
Uncle Tom	,,	1856	BB	*Early Beauty*	,,	1903	pink
Roi des Belges	,,	1860	red	*Pink Pearl* *	,,	1905	,,
Flevo	,,	1862	white	*Prince Henry*	,,	1910	yellow
Garibaldi †	Hair	1869	red	*Red Star*	M	?	red
Salmonetta	,,	1870	salmon	*Pr. Irene*	Hair	1945 ?	,,
Loveliness	,,	1870	B	Cynthella :			
Sir W. Mansfield †	U	1873	purple	*Cape Town*	Hair	...	red
Laura	Hair	1875	lilac	*Orange Queen*	,,	...	salmon
La Victoire *	S	1875	red				

B. Triploids : 12L+6M+6S = 24 (22 varieties, 6 mutants)

Anne Marie	RH	1765 ?	pink	*Bismarck* *	Hair	1875	B
Gigantea rosea	M	1857	,,	*Moreno* *	D	1878	pink
Marie	D	1860	BB	*Pr. Victoria* (C)	Hair	1879	,,
Lord Derby	D	1860	B	*Electra* †	D and M	1880	B
K. o. Blues *	M	1865	BB	*Pink Perfection*	Hair	1885	pink
mutants :				mut. *Marconi* *	D	1900	,,
K. o. Lilacs	Hair	1883	lilac	*Dreadnought*	Hair	1900	B (d)
Q. o. Pinks *	M	(1903)	pink	*Jan Bos* †	,,	1910	red
Purple King	Hair	(1909)	purple	*Pr. Margaret*	,,	1925	pink
Ivanhoe	Hair	(1920)	BB	*Wedgwood*	,,	?	B
Fireball (C) †	,,	1867	red	*Gerrit van der Mey*	,,	...	pink
Lady Derby *	M	1869	pink	*Perfection* (C)	,,	...	red
Grand Maître *	,,	1870	BB	*Rosabella* (C)	,,	...	pink
mut. *Gen. de Wet* †	,,	(1901)	pink	*Cyclop* (C)	,,	1950	red
,, *Giganteus*	,,	(1874)	,,				

* Best 15. † Second 15 varieties in 1938 according to Krelage.

(fig. 2). The evidence needs and deserves re-examination but the variety seems to be lost.

TABLE 1 (*continued*)

Name	Author	Date	2n	Complement			Colour
				L(L^a)	M	S(S_2)	
C. Unbalanced : Hypo-triploids (9 varieties)							
Rosalie	Hair	1935?	17	9(3)	4	4(2)	pink
Nimrod †	D	1858	19	11	4	4	,,
Cinderella (C)	Hair	?	19	11(3)	4	4(2)	,,
Rosea maxima	M	1866	20	10	5	5	,,
van Speyk	,,	1840	21	10	6	5	B
L'Ordre Parfait	,,	1874	22	11	6	5	?
Imperator †	Hair	1903	23	11	6	6	pink
Pres. Roosevelt	,,	1905?	23	12(3)	5	6(3)	pink (d)
C. o. Haarlem *	D, H	1893	23	12(3)	6	5(2)	yellow
D. Unbalanced : Hyper-triploids (16 varieties, 2 mutants)							
Ostara	RH	...	25	12(3)	7	6(3)	B
Maryon (C)	Hair	...	25	12(3)	7	6(3)	BB
Blue Herald	RH	...	26	13	7	6	B
La Peyrouse	D	1845	27	14	6	6	B
Card. Wiseman	M	1881	27?	12	8	7	red
L'Innocence *	D, H	1863	27	15(4)	6	6(3)	white
mut. *Mme. Sophie*	Hair	...	27	15(4)	6	6(3)	white (d)
Dr Lieber *	RH	1901	27	15	6	6	B
Schotel	Hair	1863	27	15(3)	6	6(2)	B
Fair Ellen (C)	,,	...	27	15(3)	6	6(2)	B
Q. o. Blues †	,,	1878	27	15(3)	6	6(2)	B
mut. *Q. o. Whites* *	,,	(1908)	27	15(3)	6	6(3)	white
The Bride (C)	,,	...	27	15(3)	6	6(3)	,,
A. Arendsen *	D	1875	28	14	6	8	,,
Garrick	M	1848	28	15	6	7	B (d)
La Grandesse †	M	1863	28	15	6	7	white
Edelweiss	Hair	...	28	15(4)	6	7(3)	,,
Hoar Frost	,,	...	28	16(4)	6	6(3)	,,
E. Unbalanced : Hypo-tetraploids (15 varieties)							
D. o. Westminster †	RH	1920	29	15	7	7	BB
D. o. York	Hair	...	29	15(3)	7	7(3)	mauve
Gen. Köhler	,,	1897	29	15(3)	7	7(3)	B (d)
Blue Beard	,,	1940?	29	15(3)	7	7(3)	B
Hindenburg	,,	1930?	29	16(4)	7	6(3)	B
Grace Darling (C)	,,	...	30	15(3)	8	7(3)	B
Chestnut Flower	,,	1880	30	15(3)	8	7(3)	pink (d)
Delft Blue	,,	...	30	15(3)	8	7(3)	B
Myosotis †	,,	1910	30	15(4)	8	7(3)	B
Totula	D	1913	30	15	7	8	B
Mr Dames †	RH	1910	31	16	8	7	pink
Perle Brillante †	Hair	1895	31	16(4)	8	7(3)	B
Dr Stresemann	,,	1930	31	16(4)	8	7(4)	B
Winston Churchill	,,	1945?	31	16(4)	8	7(4)	B
Springtime (C)	,,	...	31	16(4)	8	7(4)	B

(iii) *Dr Stresemann* is described in Van Tubergen's catalogue of 1936-37 as "a greatly improved *Queen of the Blues*." Since it has gained four chromosomes we may take this as a figure of speech. It is no doubt a seedling, not a bud sport. *Winston Churchill* seems to be its post-war synonym.

4. BALANCE IN THE UNBALANCED VARIETIES

We know a great deal about the distributions of chromosomes varying in total number in the gametes and zygotes produced by polyploids. We know very little, however, about how particular types of chromosomes vary. Their distributions have been accurately studied in the pollen grains of triploid hyacinths by Darlington and Mather (1944). We showed that unbalanced multiples of the chromosome set were as satisfactory, or nearly so, as the balanced multiples, thus indicating that each chromosome was internally balanced to an unusual extent. Yet the different types of chromosome such as M and S still showed (by a correlation in frequency) some dependence on one another.

We want now to carry this study further with the varieties themselves. The commercial varieties have been selected for vitality and so should give us an indication of what balances or combinations are favoured in the body cells as a permanent basis of growth.

The diploid and triploid varieties of course tell us nothing new. The intermediate unbalanced varieties on the other hand are something unprecedented among cultivated plants. The existence of such a range of unbalanced numbers in successful clones indicates that variations of number arising somatically might well maintain themselves. Differences of number in different determinations of the same variety are therefore no doubt sometimes valid. Changes of number should sometimes be associated with phenotypic mutations or divergences from description as indeed they appear to be in the suggested origin of *Marconi* and of *Madame du Barry*.

Now the unbalanced varieties have been selected in competition with the balanced varieties by breeders who were, of course, quite unaware of what they were selecting. What advantage can they have? Merely, it would seem, the *choice* of new balances that they offer. This choice, if it is effective should give a non-random sample of the population as opposed to the random sample of chromosome combinations expected from breeding the triploid varieties which must usually or originally have been their parents.

When the L chromosomes are considered in number relation with M and S in the varieties we find an obvious correlation in the whole range from diploid and tetraploid. When, however, the square is divided into four it is seen at once that the correlation depends partly on the exclusion of the 4 : 2 and 2 : 4 types of unbalance found in two of the quarters. The other two quarters where the

limits of unbalance are 3 : 2 and 4 : 3 are, however, far from evenly filled. It is not so much that they show any general correlation as that certain combinations are overwhelmingly preferred (fig. 3).

What does this preference depend on? To find out we must examine the detailed relationships of the chromosomes. Darlington and Mather noticed a preference for even numbers of M chromosomes in the nine varieties they considered. With the 36 varieties we now have this preference is confirmed. But the preference of S and L chromosomes for odd numbers is almost as striking (table 2A). The

TABLE 2A

Frequencies of chromosomes of each type in 36 unbalanced varieties (omitting 4 synonyms, from table 1c, d and e)

Nos.	4	5	6	7	8	Totals			Mean
						Odd	Even	Extra chrs.	
M	3	2	15	8	8	10	26	*96*	2·5
S	3	4	11	17	1	21	15	*81*	2·3

Nos.	8	9	10	11	12	13	14	15	16				
M+S	3	0	1	4	7	6	5	10	0	20	16	*177*	4·8
L	0	1	2	3	4	1	2	17	6	22	14	*213*	5·9

frequency of M and S chromosomes is the same but they are differently distributed. They are also correlated (table 2B).

The relations of the two types of L chromosome, again, indicates non-randomness. There is a great concentration at the level of 15 L+L^n chromosomes. There is also an avoidance of the 4 L^n type. This is not the first indication we have of a disadvantage in an increase of nucleolar organisers with polyploidy. *Paris quadrifolia* which is an undoubted tetraploid, has two, not four, nucleolar organisers. Moreover, since the substances organised in nucleoli and in the heterochromatin are similar it is interesting to notice a relationship with the decrease of heterochromatin in polyploid species of the *Paris-Trillium* group (Darlington, 1941).

So far as their external relations are concerned the L chromosomes are more numerous than M and S combined. (table 2A). The reason for this might lie in the more frequent loss of M and S chromosomes at meiosis : its source would then be mechanical rather than selective. The failure to produce a complete tetraploid itself can, however, scarcely arise from this loss : 4 M and 4 S chromosomes have not yet appeared in the same plant but, as we shall see, the necessary germ cells are produced.

In general, the evidence suggests that the uneven distribution of chromosome complements is due to a *selective concentration* on certain types rather than to accident or drift.

TABLE 2B

Correlation or selective concentration of extra M *and* S *chromosomes in 36 unbalanced varieties (from table 1c, d and e)*

4			1	1	0
3			3	4	9
2	0	1	6 / 1	3	0
1	0	1	3		
0	3	0	0		
S / M	0	1	2	3	4

TABLE 2C

Combinations of L *and* L^n *chromosomes determined in 22 unbalanced varieties (from table 1c, d and e)*

L^n \ L	6	7	8	9	10	11	12	Total	Extra chrs.
2	...	...	...	...	×	×	×	*0*	0
3	1	...	1	3	...	...	9	*14*	14
4	×	×	×	...	...	3	5	*8*	16
Total . .	*1*	*0*	*1*	*3*	*0*	*3*	*14*	*22*	30
Extra chrs. .	0	0	2	9	0	15	84	110	...

Mean extra chromosomes per variety : L-5·00, L^n -1·36.
× : types impossible within the limits of balance shown by fig. 3.

5. THE EFFECTS OF SELECTION

(i) *Historical change*

If we examine the times of origin of varieties with different numbers we see that the highest numbers seem to have arisen only in recent years (table 1 and fig. 3). This can hardly be due to the high-number group being short-lived, for nearly all recent varieties belong to this group.

We can assume that the universal habit of plant breeders of breeding from the best has been followed. In most plants where the best are triploids the practice is disastrous. In the hyacinths, on the other hand, it has evidently been successful. We may therefore imagine the following steps :—

(i) $2x \times 2x \longrightarrow 2x$ (1550-1850)
(ii) $2x \times 2x \longrightarrow 3x$ (1700-1900)
(iii) $2x \times 3x \longrightarrow 2\text{-}3x$ (1800-1920)
(iv) $3x \times 3x \longrightarrow 2\text{-}4x$ (1850-1920)
(v) $3\text{-}4x \times 3\text{-}4x \longrightarrow$ nearly $4x$ (1900-1950)

This history is sharply contrasted with that of the tulips and daffodils. Indeed, it differs from that of any other known cultivated plant in its easy transition. It does so owing to the fact that in the hyacinth all viable numbers, if not all combinations, of chromosomes have so far proved fertile.

(ii) *Present-day varieties*

We can now interpret the historical development of the hyacinth in relation to general horticultural value. Take, for example, the important varieties in cultivation in Holland in 1938 from Krelage's list (table 3). Of the 36 varieties given by Krelage, 3 are bud sports,

TABLE 3

Distribution of chromosome numbers in hyacinths according to the area cultivated in 1938 (from tables 1 and 4, cf. *fig. 2 and from Krelage, 1946, p. 636)*

	2x	17-23	3x	25-28	29-31
First 15	4	1	6	4	0
Second 15 . . .	5	2	2	3	3
Total best varieties : 30 .	9	3	8	7	3
Outsiders counted : 57 .	23	5	8	9	12

and 3 are unknown for number. The remaining 30 may be compared with the 57 varieties not mentioned by Krelage but whose chromosome numbers have been counted as in table 3 and fig. 3.

The 57 outsiders include both extremes : many of the older

diploids have dropped out of the first rank in cultivation. The newer varieties with 29, 30 and 31 chromosomes on the other hand, have not yet reached this rank.

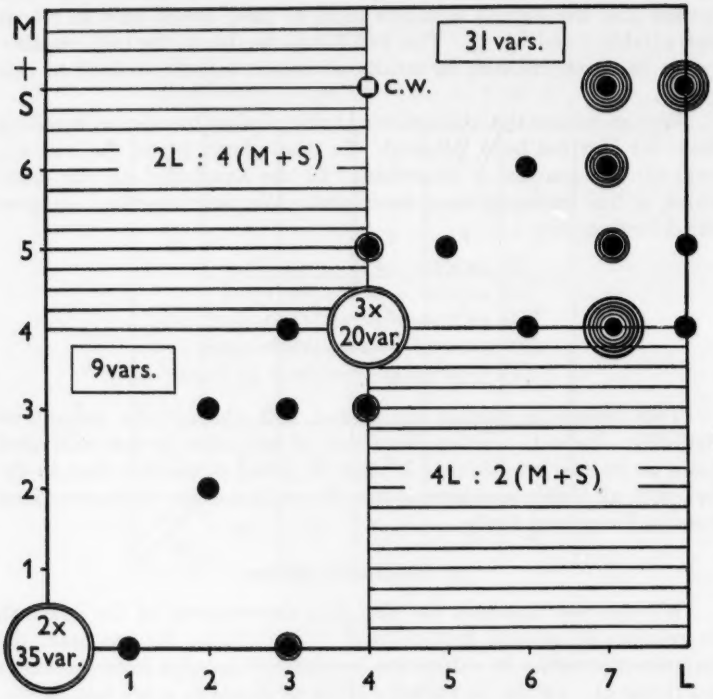

FIG. 2.—Graph showing the relations of L to M+S in the extra chromosomes of hyacinth varieties. C.W. : the dubious *Cardinal Wiseman*.

(iii) *Colour and chromosome number*

So far as we can see, any colour can be obtained with any chromosome number. But in fact the frequencies of colours change, and change in a very regular way, with chromosome number (table 4). Again there is a selective concentration. Among diploids the predominant colour is red, the proportion of blues being only 15 per cent. This proportion increases steadily to 80 per cent. in the highest group, that with more than 29 chromosomes. A possible explanation which suggests itself is the following :—

The higher chromosome numbers being the more recent, blue varieties have been introduced more than other colours in recent years (whether on account of fashion or of greater vigour, as Hibberd suggested) and thus have come to be associated with the higher

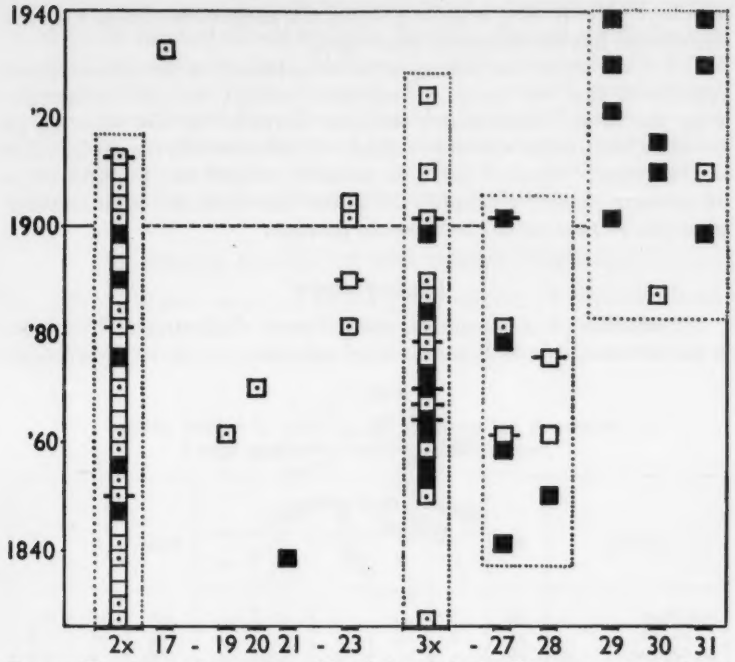

FIG. 3.—The chromosome numbers of hyacinth varieties (seedlings, not mutants) shown, in relation to their colours, date of introduction and economic value. *Blue* is solid, *red* dotted, other colours white. Included in the best 15 varieties in 1938, from Krelage's list, winged.

TABLE 4

Colours of varieties and their colour-changed mutants (when known) arranged by chromosome number (from Table 1).

In brackets are the varieties introduced since 1900

	A : 2x	C : 17-23	B : 3x	D : 25-28	E : 29-31	Total	Total since 1900
White . .	2	...	...	7	...	9	...
B and BB . .	5 (1)	1	9 (1)	9 (1)	12 (7)	36	10
Lilac . . .	3	...	2	...	1	6	...
Red and pink .	17 (4)	6 (2)	16 (3)	1	2 (1)	42	10
Salmon . .	3	...	...	...	...	3	...
Yellow . .	3 (1)	1	...	...	...	4	1
Total . . .	*33*	*8*	*27*	*17*	*15*	100	21
Blue/Total . .	15·3%	12·5%	33·3%	52·9%	80·0%	%	
Blue/Total since 1900	16·6%	...	25%	...	87·5%	%	

numbers. But in fact, as table 4 shows, the proportion of blue varieties introduced has not increased since 1900.

Thus we are driven (failing any other solution) to the extraordinary conclusion that the mutant (non-blue) colours are less compatible with the raised chromosome numbers required by the selection of breeders, than is the wild type colour. In other words, the explanation of the greater vigour of the blue varieties pointed out by Hibberd is an inherent physiological property of the blue gene not in an absolute sense but in relation to chromosome number.

(iv) *Leaf number*

A secondary but not uninteresting feature of selection in hyacinths is the leaf number. St Simon pointed out what the earlier illustrations

TABLE 5

Variation in leaf number of first size bulbs of hyacinth varieties from Messrs Suttons trials (6th April 1950) *

Variety	2n	Leaf number					Total	n	M
		7	8	9	10	11			
Pink Pearl	16	...	11	2	1	...	*116*	14	8·3
La Victoire	16	1	5	3	1	...	*84*	10	8·4
Lord Balfour	16	...	...	3	4	...	*67*	7	9·5
All 2x		1	16	8	6	...	267	31	8·6
Bismarck	24	...	...	1	...	...	*57*	7	8·1
King of the Blues and mutants	24	1	24	17	4	...	*392*	46	8·5
Lady Derby	24	1	6	10	1	...	*155*	18	8·6
Jan Bos	24	...	...	3	2	4	*91*	9	10·6
All 3x	...	2	35	31	7	4	695	80	8·7
Queen of the Blues	27	2	3	...	...	...	*38*	5	7·6
L'Innocence	27	14	12	4	...	...	*230*	30	7·7
Dr Lieber	27	5	2	...	...	...	*58*	7	8·3
Myosotis	30	3	8	1	...	...	*94*	12	7·8
Dr Stresemann	31	2	8	2	...	...	*96*	12	8·0
Perle Brillante	31	4	4	...	...	...	*60*	8	7·5
All 3x+	...	29	36...	7	...	...	576	74	7·8

confirm, namely, that the commonest leaf number in flowering hyacinths in early times was six. Modern hyacinths of full size,

* We are much indebted to Mr A. P. Balfour and his colleagues for helping us to make these records.

however, have an average of about eight and a maximum leaf number of eleven is reached in one triploid, *Jan Bos*. Second size bulbs have from 0·4 to 1·2 leaves less. The unbalanced varieties with the largest flowers which have been raised in the last century seem to have slightly fewer leaves than the old balanced varieties (table 5). The five double varieties we have had in cultivation in 1951—two triploid and three hypertriploid—had 115 leaves on 17 bulbs, an average of 6·8, lower that is, than any single-flowered variety.

6. POLLEN GRAINS OF THE NEAR-TETRAPLOIDS

The extensive counts of pollen grain mitoses of triploids carried out by earlier workers have shown an almost complete absence of abnormality. The consequences of crossing-over in inversions so

FIG. 4.—Proportionate complements at pollen grain mitosis. Above, a haploid set in *Anne Marie*. Left, 6 : 3 : 3 complement from *Duke of Westminster*. Right, a complement with balanced diploid number but unbalanced types resulting from chromatid non-disjunction in *Duke of Westminster*. Acetic-alcohol-Feulgen preparations. ×1500.

freely found in triploid tulips (Upcott, 1939) or daffodils (Wylie, 1949) rarely appear in hyacinths, whose stability in this respect exceeds what is needed to account for the stability of the chromosomes in the varieties. The problem is, therefore, merely one of individual distribution.

Our observations of the pollen grains have been limited to from 56 to 124 mitoses in 15 of the triploid and hyper-triploid varieties we have studied (tables 6 and 7). These numbers do not allow of the statistically valid inference of chromosome interactions. They show, however, that the distributions follow the principles laid down by Darlington and Mather, *viz.*: an increasing frequency of loss with decreasing size of the chromosome. All our counts, however, show less loss than the previous counts of triploids—even our own triploid. In the near-tetraploids, quadrivalents must be subject to less loss than trivalents.

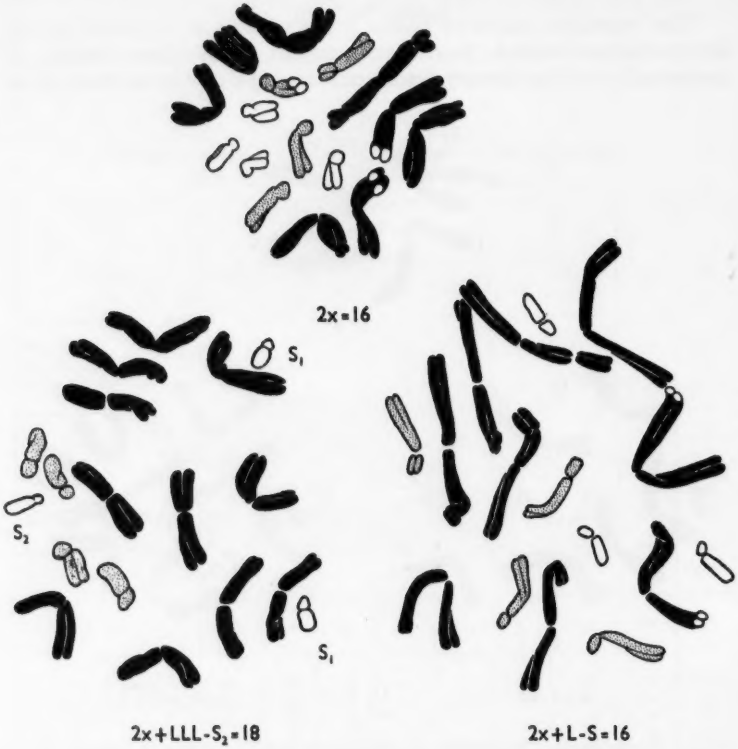

FIG. 5.—Three pollen grain mitoses of *Mr Dames* with balanced diploid, unbalanced diploid and hyperdiploid numbers. ×1500.

Pollen grains with more than the diploid total number were found in the near-tetraploid varieties. On the other hand, chromosome complements with more than the diploid number for one chromosome type and less for another (*i.e.* in 3 : 1 unbalance) were common (figs. 4 and 5).

It might be argued that these suggest the possibility of such an unbalance in the somatic complement of a variety. But there is a difference between carrying out a single pollen grain mitosis (which is possible for an under-haploid nucleus, *cf.* Conger, 1940) and maintaining the whole sequence of development and the efficiency

TABLE 6

Counts of pollen-grain mitoses in hyacinth varieties showing the distribution and loss of extra chromosomes (1948)

Variety	2n	No. of P.G.	8	9	10	11	12	13	14	15	16	17	Mean no. of chrs. in P.G.	Estimated loss (per cent.)
Earlier 3x *	24	556	5	36	92	136	132	102	43	6	4	...	11·59	10·15
Anne Marie	24	69	1	4	5	17	21	12	7	2	...	...	11·8	5·0
Ostara	25	124	...	...	12	21	25	27	29	8	2	...	12·6	...
Blue Herald	26	60	...	1	4	7	12	13	14	6	3	...	12·9	1·9
Dr Lieber, *Schotel*, *L'Innocence*, *Q. o. Blues*, *Q. o. Whites*	27	301	...	...	2	11	53	98	78	48	11	...	13·4	1·8
Duke of Westminster, *Blue Beard*	29	109	...	...	...	...	7	18	38	33	12	1	14·2	3·5
Delft Blue	30	56	...	...	...	...	...	3	15	22	9	1	14·8	2·6
Dr Stresemann, *Perle Brillante*, *W. Churchill*	31	261	...	...	...	...	...	17	53	97	60	44†	15·3	2·5

* Belling, 1924; Darlington, 1926; Darlington and Mather, 1944.
† Including three with 18 and one with 19.

TABLE 7

Variation in numbers of chromosomes of each type in the pollen grains of 3x and aneuploid varieties. Numbers beyond the disomic number in italics (part of data in table 6)

	L									M						S			
	2n+	4	5	6	7	8	9	10	11	2n+	2	3	4	5	6	2n+	2	3	4
Electra	(4)	13	42	**58**	50	12	...	...	...	(2)	**70**	60	45	...	...	(2)	**85**	63	27
Anne Marie	(4)	3	15	**29**	20	2	...	...	...	(2)	21	**27**	21	...	...	(2)	**29**	25	15
Ostara	(4)	2	15	**22**	15	9	...	...	...	(3)	1	**31**	30	*1*	...	(2)	**30**	24	9
Blue Herald	(5)	2	11	**19**	18	8	*2*	...	...	(3)	3	29	27	*1*	...	(2)	17	**24**	19
Dr Lieber, *L'Innocence*	(7)	...	3	15	**50**	40	*2*	...	...	(2)	33	**51**	33	...	...	(2)	42	**46**	29
D. o. Westminster	(7)	...	*1*	7	**23**	21	*4*	*1*	...	(3)	...	24	**29**	*3*	*1*	(3)	7	**32**	18
Mr Dames	(8)	...	...	*1*	9	17	*21*	*2*	*1*	(4)	1	7	**38**	*5*	...	(3)	4	**32**	15

of protein production in the body of the plant. These mitoses are interesting, however, in other ways. They show that in other plants, where the types are not distinguishable, a balanced chromosome number may conceal a genuine unbalance.

Unbalanced pollen grains are also interesting in showing extreme abnormalities in the segregation of multivalents, *e.g.* the pollen grain

of *Duke of Westminster* (15 : 7 : 7) which had 7 : 6 : 3 chromosomes (fig. 5 and tables 6 and 7). Here there must have been 1 M^{iv}+1 M^{iii} at meiosis and of these seven chromosomes, or more strictly fourteen chromatids, six entered one pollen grain. Such an inequality can have arisen quite simply in this way: one M univalent might be included double or undivided to give two chromosomes in one nucleus. Two trivalents might then divide into 2+1. Thus a nucleus might have a legitimate segregation of four, together with an illegitimate inclusion of two, chromosomes. The complete tetrad would then

TABLE 8

Summary of table 7

Type	No. of varieties	No. of cells	Extra chromosomes			Proportion realised	No. of chromosomes
			Somatic	Pollen grain			
				Mean expected	Mean observed		
L	3	307	*4*	2·0	2·075	**1·04**	614
	1	60	*5*	2·5	2·417	**0·97**	150
	3	174	*7*	3·5	3·345	**0·96**	608
	1	51	*8*	4·0	3·941	**0·99**	204
M	4	361	*2*	1·0	0·931	**0·93**	361
	3	180	*3*	1·5	1·528	**1·02**	270
	1	51	*4*	2·0	1·921	**0·96**	102
S	6	484	*2*	1·0	0·787	**0·79**	484
	2	108	*3*	1·5	1·204	**0·80**	162

have the constitution in respect of M chromosomes: 6+4+2+2 = 14. The conditions for this inequality of distribution are found at meiosis in aneuploid hyacinths (Darlington, 1929). It is also to be noted that this extreme inter-type unbalance is found in respect of the M chromosomes which, as we saw earlier, may well have a mutually dependent or intra-type balance.

The finding of genuinely balanced diploid pollen grains shows that in the course of breeding the modern varieties with 30 and 31 chromosomes true tetraploid seedlings must often have been raised. They must have been rejected as commercial varieties. Perhaps the mechanical limit to the number of chromosomes which can be conveniently accommodated in the cells available has been reached—for the time being.

7. SUMMARY

1. The garden hyacinths have been selected for increase in size and chromosome number and for variety of colour since they were introduced to Europe in 1560.

2. In the haploid set of eight there are five distinct chromosome types. Among over 2000 chromosomes recorded in 106 varieties only four have been of abnormal shape. This uniformity agrees with the documentary evidence in pointing to a highly homogeneous origin.

3. The 106 varieties are constituted as follows :—

	2x = 16	17-23	3x=24	25-31
Seedlings . .	35	9	22	31
Bud sports . .	1	0	6	2

The occurrence of such a series of unbalanced combinations is unique among all plants and animals.

4. The loss of chromosomes at meiosis is highest for the short type, lowest for the long, in the unbalanced as well as in the triploid varieties.

5. The limits of unbalance are strictly set and ascertainable since 5 chromosome types are recognisable. Although pollen grains can have a 3 : 1 unbalance, the 4 : 2 unbalance does not occur somatically, and varieties are limited to 4 : 3 and 3 : 2. There is also strong *selective concentration* on certain types of unbalance.

6. The selection of the varieties rather than of their parental gametes is responsible even for the notable absence of the balanced tetraploid combination.

7. Blue has been progressively more favoured at the expense of other flower colours as the chromosome number has been raised by selection during the last 100 years. Its advantage, noted in 1880, has been due to physiology, not to fashion.

8. Of the 5000 garden hyacinths raised, less than 100 varieties are known to survive. Additions to this number would (we have tried to show) be a gain to science.

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Plate

Microphotographs of root-tip mitoses in varieties of hyacinths, pre-treated with mono bromonaphthalene and Feulgen stained. ×1600.

1. *Distinction*, mutant cell in the normal diploid : 2n = 16.

In this cell the L^n chromosome at 9 o'clock has gained in its distal segment probably by interchange with another chromosome : the only aberrant cell seen in our studies.

2. *Scarlet O'Hara*, alias *Madame du Barry* : bud sport of *Distinction* : 2n = 16, one L deficient : the reciprocal condition to that shown above but characteristic of the whole clone.

3. *Rosalie* : 2n = 17 ; 3 L^n chromosomes show their nucleolar constrictions.

SOMATIC AND SECONDARY PAIRING IN *ORNITHOGALUM*

EEVA THERMAN

State Horticultural Institute, Piikkiö, Finland

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1. INTRODUCTION

CONSIDERING the great amount of cytological work done on Liliaceous plants, the genus *Ornithogalum* has remained comparatively neglected. The chromosome number has been determined in several species, but the genus as a whole has not been the subject of cytological analysis. From the papers of Delauney (1927), Heitz (1926), Geitler (1929), and Nakajima (1936) it is seen that the chromosome numbers vary considerably in the different species. So far the following diploid numbers, which seem to fit into an aneuploid series, have been encountered : 10, 12, 14, 16, 18, 24, 27, 30, 32, 50, 54.

The present study deals with the cytology of two *Ornithogalum* species, *O. graminifolium* Thunb. ($2n = 10$) and *O. caudatum* Ait. ($2n = 54$), both native to the Cape. The distinguishing feature in their chromosome behaviour is a strong tendency to somatic and secondary pairing. This feature, which has been overlooked by the earlier investigators of the genus, might prove a valuable tool in a comparative study of cytogenetic relations in the genus *Ornithogalum*. That such a study would yield interesting results seems evident, not only on account of the fragmentary knowledge of the chromosome numbers, but also from the taxonomy and the geographical distribution of the genus (*cf.* Baker, 1873 ; Feinbrun, 1941). Of the 73 species recognised by Baker, 39 belong to the Cape, a few species are native to tropical Africa, one grows in Chile and Peru, and the rest are spread around the Mediterranean.

2. MATERIAL AND METHODS

Both mitosis and meiosis were studied in *Ornithogalum graminifolium* (Botanical Garden of Coimbra) and *O. caudatum* (Botanical Garden of Pisa). The plants were received as bulbs and cultivated in a hot-house at a suitable temperature. The somatic chromosomes of *O. graminifolium* were examined in acetic-alcohol-Feulgen squash preparations made from root tips (*cf.* Darlington and La Cour, 1947). Slides made according to this method were not very favourable for the demonstration of the somatic pairing of the chromosomes. Unfortunately the plant in question had died before this cytological feature had been discovered. Additional material could therefore not be obtained. Meiosis in the PMC was studied in smear preparations, a part of which had been fixed in acetic-alcohol and stained with Feulgen. Another part was fixed in La Cour's 2 BD and stained with crystal violet.

The root tip mitoses of *O. caudatum* were studied both in squashes made as above and in sectioned material fixed in 2 BD and stained with Feulgen. The PMC were made into preparations by the same methods as in *O. graminifolium*. The magnification of the camera lucida drawings is ×2000, that of the microphotographs being about the same.

3. OBSERVATIONS

(I) Ornithogalum graminifolium

Mitosis.—This species has five pairs of somatic chromosomes, three pairs of which are long and two pairs short. The homologous chromosomes show a great tendency to somatic pairing. This is seen in prophase where the chromosomes, as a rule, lie in pairs. This phenomenon is, however, more easily examined in metaphase (fig. 1*a*), different metaphase plates showing variation in this respect. The same tendency gives a characteristic appearance also to the mitotic anaphases. Anaphases and telophases often exhibit chromatid bridges between the separating chromosome groups (fig. 1*b*). In interphase nuclei some ten chromocentres and two nucleoli are visible.

Meiosis.—In pachytene the chromocentres appear as more condensed parts in the thread-like chromosomes. They seem to vary slightly in number between eight and ten, in any case exceeding the bivalents in number. The big chromocentre (fig. 1*c*, at 4 o'clock) is constant in appearance, and it could be distinguished in all the nuclei examined. The chromocentres do not show any tendency to run together, appearing in fact, even more condensed than other chromosome regions.

Though the pachytene stages in this plant cannot be analysed as elaborately as has been done by Coleman (1940, 1941) in *Veltheimia* and *Rhoeo*, it is obvious that the chromocentric regions, as in these plants, are tightly coiled parts of the chromosomes. Consequently they are incapable of real pairing. This is especially clear in the big chromocentre mentioned above, which in most cells reveals a distinctly bipartite structure.

In diakinesis the chromosomes in most cells form three large and two small bivalents. Not uncommonly, however, one or more chromosome pairs remain as univalents. The univalents then show the same general repulsion as the bivalents. An example of such a diakinesis stage is seen in fig. 1*d*. One of the short chromosome pairs has remained unpaired, and the two univalents lie on opposite sides of the cell.

The first meiotic metaphase exhibits several features which deviate from the normal. Fig. 1*e* illustrates the most regular type of metaphase plate found in *O. graminifolium*. In this case all the chromosomes have paired to form five bivalents, which are fairly regularly orientated in a metaphase plate. Disturbances in bivalent orientation are, however, common, one or more of the bivalents in many cells lying outside the plate. In the cell in fig. 1*f* one of the large bivalents is

unorientated, while the other four form a regular plate. In fig. 1*g* again we see a side view of a first division metaphase in which con-

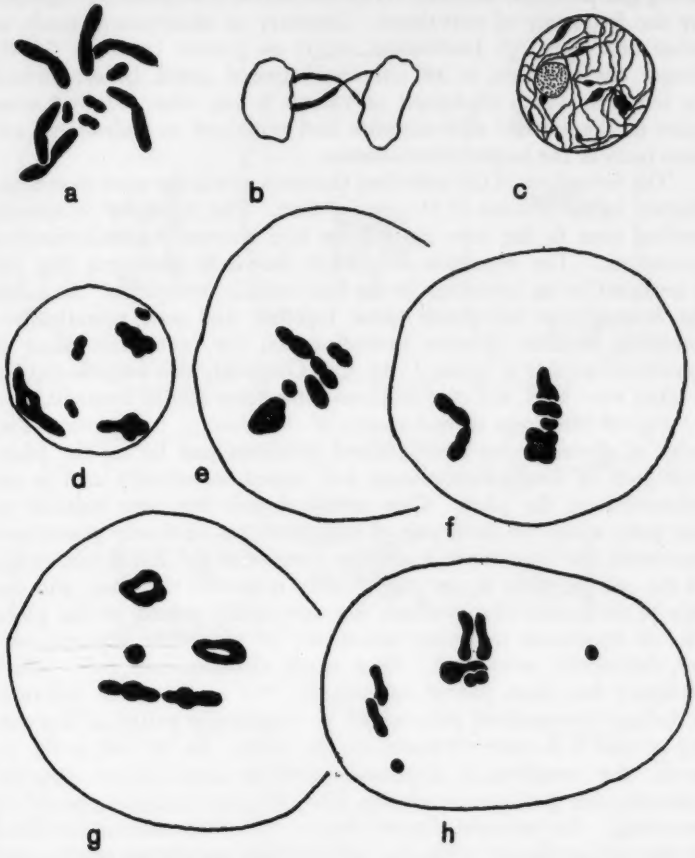

FIG. 1.—*Ornithogalum graminifolium.*

(*a*) Metaphase from a root tip cell with ten chromosomes; the chromosomes show somatic attraction.
(*b*) Telophase from a root tip cell with chromatid bridges.
(*c*) Pachytene showing a nucleolus and nine chromocentres.
(*d*) Diakinesis with four bivalents and two small univalents.
(*e*) Metaphase I with five orientated bivalents.
(*f*) Metaphase I with five bivalents, one lying outside the plate.
(*g*) Metaphase I with five unorientated bivalents.
(*h*) Metaphase I with two bivalents and three pairs of univalents, one of which lies somatically paired on the plate, one at the one pole, while one pair is separated.

gression has failed and the five bivalents are scattered around the place where the metaphase plate ought to be situated.

Chiasma frequency in *O. graminifolium* is low. In ten cells only 45 chiasmata in all could be recorded, which gives a chiasma frequency of 0·9 per potential bivalent. The low chiasma frequency is reflected by the frequency of univalents. Contrary to observations made on other organisms (*cf.* Darlington, 1937) no greater tendency for the longer chromosomes to be effectively paired could be established. In ten cells which contained univalents it was observed that seven pairs of the smaller chromosomes had remained as univalents, and nine pairs of the larger chromosomes.

The behaviour of the univalent chromosomes is the most interesting feature in the meiosis of *O. graminifolium*. The tendency to somatic pairing seen in the root tip mitoses also governs the behaviour of univalents. The repulsion they have shown in diakinesis (fig. 1*d*) is replaced by an attraction in the first meiotic metaphase. As a rule the homologous univalents come together and pair somatically—naturally without chiasma formation—on the metaphase plate or sometimes outside it (plate I, fig. 2). Obviously this somatic pairing is often very brief, the chromosomes separating almost immediately.

Fig. 1*h* illustrates several modes of chromosome behaviour. Two pairs of chromosomes have formed bivalents and lie on the plate. One pair of long chromosomes has paired somatically and is co-orientated on the plate. One univalent pair lies close together at one pole, while the third pair of univalents has obviously paired and separated, and now shows a position correlation (*cf.* Ribbands, 1937). In the cell shown in fig. 2*a* one bivalent is outside the plate, and one pair of the longer chromosomes lies somatically paired on the plate. Fig. 2*b* represents a further metaphase in which the chromosomes are defectively orientated. One small chromosomes pair, which obviously has been paired somatically, has separated in advance. A further chromosome pair, which is somatically paired, is interesting in that it is auto-orientated on the plate. In the cell in fig. 2*c*, again, the members of the two univalent pairs lie at opposite poles showing position correlation (the cell axis is slightly twisted in smearing). An example of rarer chromosomes behaviour is furnished by the cell in fig. 2*d*. The two homologous univalents are situated on the same side of the plate ; it is not certain whether or not they have been somatically paired. In fig. 2*e* a situation is represented in which the three univalent pairs, which obviously have previously been paired somatically, are separated while the two bivalents still lie on the plate. An interesting feature makes its appearance in this cell. Usually only the somatically paired univalents seem to be capable of auto-orientation ; in this cell the upper bivalent is obviously auto-orientated. The cell represented in fig. 2*f* provides an example of great variation in the chromosome behaviour of a single cell. The large bivalent at the left contains two chiasmata. The large chromosome pair at the right has formed only one chiasma and is separating precociously. The two short chromosome pairs have paired somatically;

one of the pairs is co-orientated, while the other shows auto-orientation. The fifth chromosome pair lies separated at one of the poles. In fig. 3*a* an extreme case is illustrated. In this cell all the chromosomes

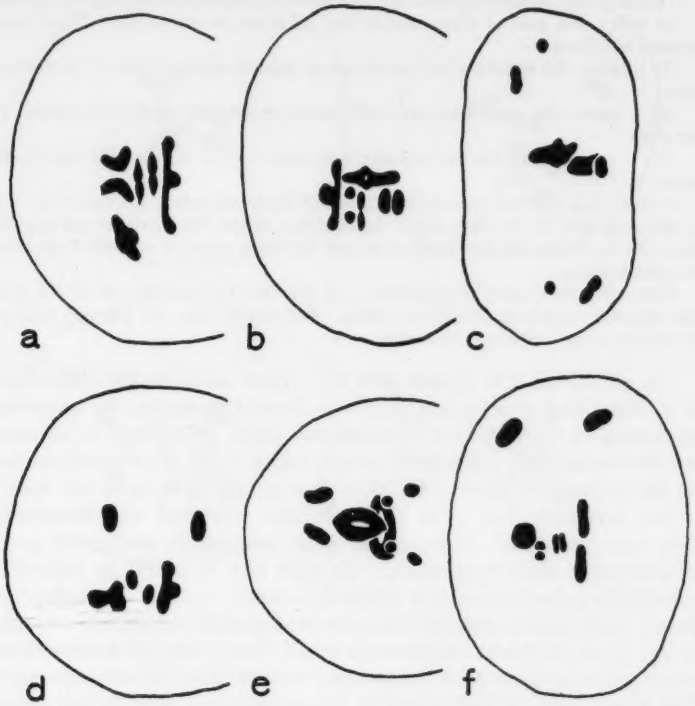

FIG. 2.—First meiotic metaphases in PMC of *Ornithogalum graminifolium*.

(*a*) Three bivalents are orientated, one lies off the plate, while the two univalents are somatically paired.

(*b*) Three bivalents, one pair of separated chromosomes; and two somatically paired auto-orientated univalents.

(*c*) Three bivalents and two pairs of separated univalents.

(*d*) Four bivalents and one pair of univalents.

(*e*) Two bivalents: the left auto-orientated, the right co-orientated; three pairs of precociously separated chromosomes, which obviously have been somatically paired.

(*f*) Two bivalents and three pairs of univalents, of which two lie on the plate and one off the plate; the right univalent pair auto-orientated.

have remained as univalents. In the first metaphase they show more or less strong attempts at somatic pairing, lying scattered around the equator.

To obtain an idea of the frequency of the various modes of chromo-

some behaviour the conditions in 71 cells at first meiotic metaphase have been analysed as follows :—

32 cells : all the chromosomes had conjugated and the five bivalents were orientated fairly regularly.

15 cells : only bivalents present but they showed disturbances in their orientation.

20 cells : one pair of chromosomes had remained as univalents. These were situated as follows :—

(i) 9 cases—the members lay correlated on opposite sides outside the metaphase plate.

(ii) 4 cases—the univalents were still paired somatically and were situated on the plate.

(iii) 7 cases—again the two univalents lay more or less side by side outside the plate.

2 cells : two pairs of univalents. In one of them one pair of the univalents was on the same side of the plate, while the members of the other pair lay on opposite sides. In the other cell the members of both the pairs occupied correlated positions at opposite poles.

One cell : three pairs of univalents. In this case the members of all the pairs were situated correlated on opposite sides. And finally, one cell (fig. 3*a*) with all the chromosomes unpaired was scored.

As seen from the figures and the above analysis the differences in pairing and orientation lead to desynchronisation in anaphase separation of the different chromosome pairs. The first to separate are the somatically paired univalents which have been co-orientated on the metaphase plate. The next to separate seem to be the halves of the bivalents, but even these do not segregate simultaneously. The auto-orientated chromosome pairs necessarily encounter great difficulties in their separation. No rule can be given in regard to somatically paired univalents which have never reached the metaphase plate ; their defective orientation also renders their separation variable. In fig. 3*b* an incipient anaphase is seen. Two pairs of chromosomes, which probably have been somatically united, have already separated. The third pair of univalents is auto-orientated and consequently shows no attempt to separate. The halves of the two bivalents are only just about to separate. It must be pointed out that the univalents, once separated, never return to the metaphase plate to divide in the first division, as is the case in many other organisms (*cf.* Ribbands, 1937).

In view of the great deviations from normal meiosis characteristic of *O. graminifolium* it is remarkable that the results of the first division are not more abnormal. This fact must in the first place be ascribed to the property of somatic attraction which allows the fairly regular somatic pairing of the univalents and their subsequent segregation. Though the chromosome pairs differ in the timing of their separation, in the end the chromosomes segregate, ensuring the formation of anaphase groups with five chromosomes each. In fig. 3*c* a regular anaphase separation is illustrated. Naturally, the unorientated chromosomes are bound to give rise to uneven chromosome numbers. That this is not, however, of very common occurrence is seen from

the normal course of the second division. A regular second division metaphase with five chromosomes in each plate is seen in fig. 3*d*. The tetrads also appear normal, no micronuclei being visible.

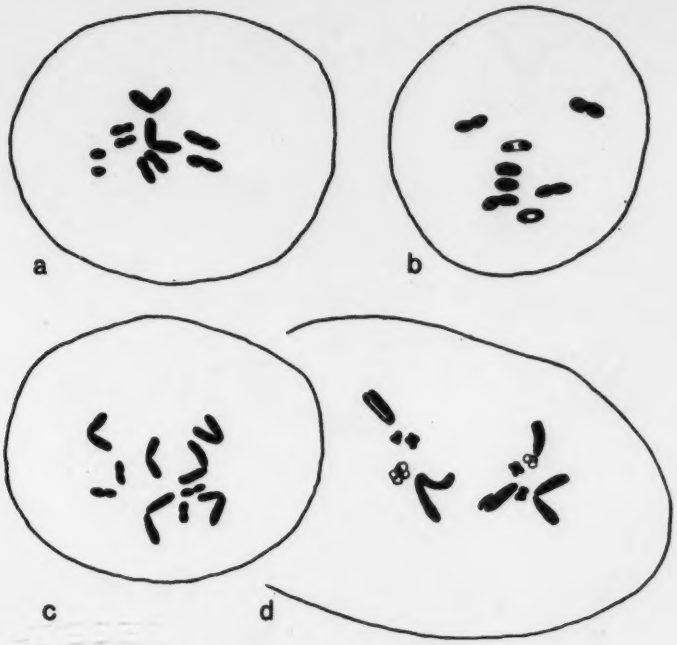

FIG. 3.—Meiotic stages in PMC of *Ornithogalum graminifolium*.

(*a*) Metaphase I showing five pairs of somatically paired univalents.
(*b*) Anaphase I with two bivalents, two pairs of precociously separated univalents, and one auto-orientated pair of univalents.
(*c*) Regular anaphase I.
(*d*) Metaphase II with five chromosomes in each plate.

(II) Ornithogalum caudatum

Mitosis.—This species possesses 54 somatic chromosomes in its root tip cells. As appears in fig. 4*a* the smaller chromosomes, especially, often lie in pairs in metaphase, thus showing, though to a lesser degree, the property of somatic pairing which is so well developed in *O. graminifolium*. The metaphase plates vary, however, in regard to the degree of somatic pairing. In the interphase nuclei in the root tips two nucleoli and about 20 Feulgen-stained chromocentres are visible (fig. 4*b*).

Meiosis.—The pachytene nuclei reveal the paired chromosome threads, in which some ten more or less condensed regions are visible (fig. 4*c*). These chromocentres are distinct in all the pachytene

stages examined, and their number is fairly constant. They do not appear to be sticky, and accordingly they do not show any tendency to run together. As meiosis proceeds the chromocentres remain

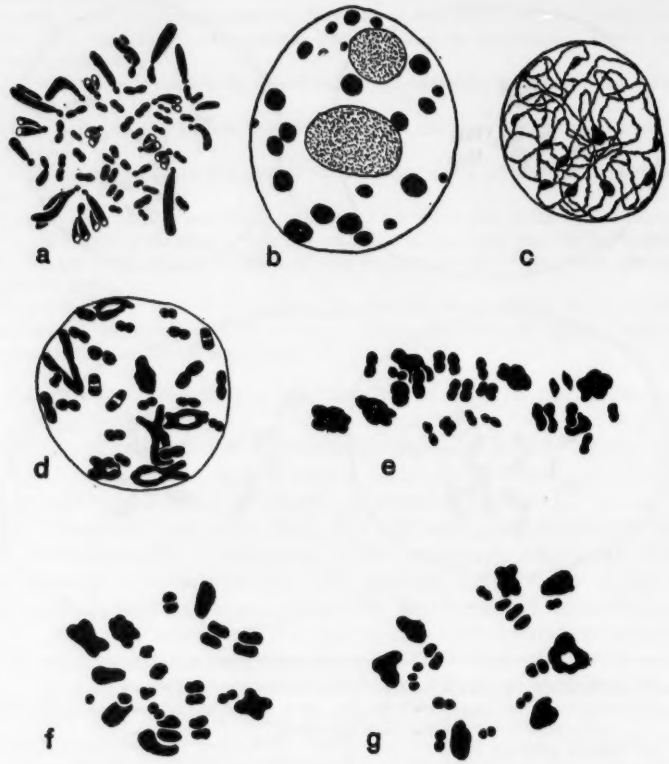

FIG. 4.—*Ornithogalum caudatum*.

(*a*) Metaphase plate from a root-tip cell with 54 chromosomes ; the smallest chromosomes lie in pairs.
(*b*) Interphase from a root-tip cell showing two nucleoli and some twenty chromocentres.
(*c*) Pachytene with eleven chromocentres.
(*d*) Diakinesis with seven large and twenty small bivalents.
(*e*) Side view of metaphase I ; the smaller bivalents show secondary association.
(*f*) Metaphase I ; the smaller bivalents are secondarily associated.
(*g*) Metaphase I ; the smaller bivalents are secondarily associated.

condensed, while the rest of the chromosomes gradually catch up with them.

In diakinesis (fig. 4*d*) 27 bivalents—7 larger and 20 smaller—are visible. They are spaced around the nuclear cavity and do not exhibit any secondary pairing.

The first metaphase, however, is characterised by a strong secondary association of the smaller bivalents (figs. 4*e*, *f*, *g*). The seven large bivalents seem to be spaced at random, whereas the twenty small ones, as a rule, lie in pairs. This is apparent in side views as well as in polar views. The different plates show slight variations in this respect, but usually the phenomenon is very regular.

The first anaphase also proceeds normally. In a few cells inversion bridges are visible. Fig. 5*a* illustrates a first division anaphase where the centromere of one chromosome has misdivided; the two longer arms are going to one pole and the two shorter ones to the other (*cf.* Darlington, 1939).

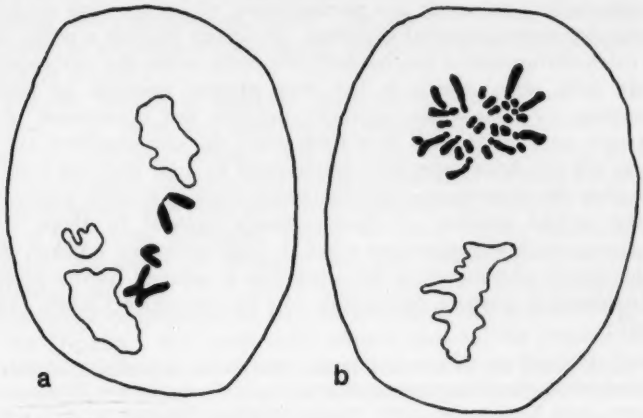

FIG. 5.—Meiotic stages in *Ornithogalum caudatum*.

(*a*) Anaphase I; the centromere of one chromosome has misdivided.

(*b*) Metaphase II; the smaller chromosomes show secondary association.

In the second division metaphases, secondary pairing is as pronounced as in the first. Fig. 5*b* represents a second division metaphase in which the smaller of the 27 chromosomes lie side by side. As a rule, the second division is regular and the tetrads also appear normal.

4. DISCUSSION

(I) *Chromosome attraction and repulsion in the light of the precocity theory*

It is a generally acknowledged fact that the mutual relations of the chromosomes in mitosis and meiosis are governed by two main forces. On the one hand, two homologous genes—and consequently the chromosomes containing them—attract each other specifically. On the other hand, the chromosomes show an unspecific body repulsion

(*cf.* Darlington, 1937). How these forces act and in what way they are interrelated with other phenomena involved in mitosis will, be discussed in the following.

In normal mitosis the intrachromosomal mechanism, *i.e.* the cycle undergone by the chromosomes, acts strictly in step with the extra-chromosomal mechanism, which is represented by the spindle. According to Darlington (1937), the meiotic phenomena can best be brought into relation with mitosis by assuming that the two mechanisms are out of step. In meiosis the external changes are precocious as compared with the internal changes. This precocity theory has been developed further by Oksala (1943, 1944). In his study on the cytology of the dragonfly genus *Aeschna*, Oksala (1944) has shown that precocity is a phenomenon which develops gradually during the spermatogonial divisions. It finally reaches a point when the extra-chromosomal mechanism acts twice while the chromosomes divide only once, which is the very process essential in meiosis. According to Oksala the precocity implies the occurrence of the polarised stage in the cell at a time when the chromosomes are still single. It has been especially emphasised by him that the question is whether the chromosomes are *functionally* single or double, irrespective of the actual number of chromonemata present in them. The effectively single chromosomes react to polarisation by pairing, while in the double chromosomes the attraction is satisfied by the presence of an identical partner chromatid. In the words of Oksala (1944) p. 26) :

" Dann würde das in frühesten Phasen der Meiose bemerkbare, eigenartige, von allen mitotischen Vorgängen krass abweichende Verhalten der Chromosomen, also gerade die Konjugation, nicht von der frühreifen Prophase, sondern von der eben in dieser Phase entstehenden frühreifen Polarität herrühren. Es würde sich mithin um eine entweder unmittelbar nach der Telophase oder in der frühen Interphase entstehende Metaphasesituation handeln, auf die die einfachen Chromosomen durch Konjugation reagieren und so die Doppelgestalt und zugleich also die Fähigkeit der polaren Orientierung erlangen."

It may be mentioned in this connection that Klingstedt (1939), on the basis of certain purely morphological similarities, came to the conclusion that leptotene and metaphase are related stages.

As a rule, the attraction of homologous chromosomes seems to be saturated in the double chromosomes in mitotic prophase and in the paired chromosomes in meiosis. We have, however, instances in which a so-called residual attraction remains, which gives rise to somatic and secondary pairing of the chromosomes. In regard to the forces concerned we may cite Darlington (1934, p. 107) :

" It is then possible to suppose that a common force of attraction exists between identical genes and that this attraction is almost or entirely saturated by the approximation (or association) of genes in pairs. Secondary attraction, A_2, is then a residual attraction and its variation is merely the variation of degree of saturation by pairing. In meiosis in the male *Drosophila* the saturation reaches its

lowest level. Forces of repulsion due to surface charge (R_1) and localised charge at spindle attachment (R_2) and spindle poles (R_3) can likewise all be considered most conveniently as a unit in regard to physical causation."

As was mentioned above, one of the results of residual attraction is the somatic pairing of the chromosomes. This involves a tendency of the homologous chromosomes to be situated closer together than non-homologous chromosomes during mitotic stages. This phenomenon is to a slight degree revealed by many organisms. To prove it, in many cases a statistical analysis of the frequency of the various chromosome arrangements in metaphase would be needed (*cf.* Upcott, 1936). Somatic pairing is very pronounced in polyploid plant cells which have arisen due to endomitosis, a condition realised, for instance, in many Chenopodiaceous plants. In the metaphase following the endomitotic chromosome doubling, the homologous chromosomes lie regularly in two's.

Somatic pairing is, however, most strongly developed in various Diptera. In these the homologous chromosomes, whether two or more, are regularly situated side by side. Moffett (1936), in *Culex pipiens*, has found an attraction of chromosomes at all stages of mitosis, being, however, at a minimum in metaphase. If we apply to somatic pairing the views developed above, we come to the following conclusions. It might be thought that the precocity of the external changes in the cell, which plays such a decisive role in regard to the chromosome conjugation in meiosis, also gives rise to somatic pairing in the Diptera. We need only assume that in the mitoses of the Diptera a slight precocity prevails which results in the fact that the chromosomes during the various mitotic phases are relatively single as compared with other organisms. This precocity is not strong enough to give rise to actual pairing but the functionally single chromosomes attract each other and pair somatically. This is in agreement with the fact that somatic crossing-over has occasionally been reported in *Drosophila* (*cf.* Darlington, 1937).

This ability of the chromosomes to pair somatically has provided a starting-point for the evolution of the various types of meiosis found in the Diptera which so greatly deviate from the normal (*cf.* White, 1949). In the most primitive forms chiasmata are present in both sexes ; the sex chromosomes, however, do not form chiasmata in the male. The behaviour of the sex chromosomes resembles the distance conjugation observed in the Neuroptera (Klingstedt, 1933). According to White, *loc. cit.*, two main evolutionary lines may be derived from this primitive type. In one of them chiasmata are present in the male, but the sex chromosomes have disappeared as separate units. The other line again is characterised by the fact that the sex chromosome mechanism is retained, the chromosomes in the male being, however, devoid of chiasmata. From this a side line has developed, in which the whole chromosome cycle is quite anomalous. The highest Diptera, which may also be derived from the line in which chiasma formation

fails in the male, again have a pairing segment in their sex chromosomes. A further case which possibly has a bearing on the present problem is the touch-and-go pairing of the sex chromosomes in certain Hemiptera (*cf.* Wilson, 1905 ; Darlington, 1937).

Another phenomenon which is accounted for by the residual attraction is the secondary association of the chromosomes. It is often seen, especially in plants with small chromosomes, that the bivalents are not spaced at random on the metaphase plate, but lie in twos or in groups containing more than two chromosomes. As a rule, the bivalents involved are of the same shape and size. The first to pay conscious attention to this phenomenon has been Darlington (1928) in his study on *Prunus*. Lawrence (1931) in his comprehensive survey on this subject, has presented a great number of examples in which secondary association has been described or is to be inferred. According to Lawrence the following features are characteristic of secondary association. It is not present in diakinesis, but in the first metaphase the—obviously related—bivalents arrange themselves in pairs or groups of more than two. They lie near each other, but do not touch. The same tendency is exhibited in the second meiotic division. That this attraction of certain bivalents indicates their homology seems to be an established fact (*cf.* Meurman, 1933 ; Darlington, 1937). Indeed, this phenomenon has been used to throw light on evolution and relationships in various plant groups, secondary association being regarded as a token of ancient homology of the chromosomes involved.

If we try to establish a common ground for the interpretation of the phenomena in which chromosome attraction plays a role, we come to the following conclusions. As recapitulated above, the meiotic phenomena may best be explained as a result of the precocity of the external changes in the cell. In accordance with this, somatic pairing might be regarded as due to a slight degree of precocity. This, in turn, leads to the chromosomes being either effectively single, or in a midway state between functional singleness and doubleness (*cf.* Huskins, 1948), which again gives rise to an attempt of the homologous chromosomes to pair. It seems probable that secondary association would be explicable in a like manner. A somewhat similar view has been presented by Svärdson (1941) in regard to somatic pairing in fishes belonging to the genera *Salmo* and *Coregonus*. In these animals the somatic attraction of the chromosomes is most pronounced during anaphase and telophase, and Svärdson ascribes this fact to the singleness of the chromosomes at these stages. It must finally be stressed that the views developed above represent only the basic line of thought. The interpretation of the various individual cases will certainly require additional hypotheses.

To sum up : There seems to be two main conditions determining the degree of chromosome attraction. First, we have the relative singleness or doubleness of the chromosomes. As a rule, the highest

degree of relative doubleness is reached in the metaphase stage. This obviously causes somatic pairing in many organisms to be at a minimum in metaphase (for instance, *Culex*, *Salmo*, *Coregonus*). A factor acting in the opposite direction is that the repulsion forces between the chromosomes, which are so strong both in mitotic prophase and in diakinesis, are to a considerable extent diminished when the metaphase stage is reached. It seems that the latter factor is in many cases decisive, for instance, the secondary pairing characteristic of many plants is apparent only in metaphase. In general it can be said that the degree of somatic and secondary association is the resultant of these two tendencies.

(ii) *Somatic and secondary pairing in* Ornithogalum

The chromosome behaviour in the two *Ornithogalum* species shows that the same causes bring about the same results at the cytological level in the most diverse organisms. The phenomena which the capacity for somatic pairing has made possible in *Ornithogalum*, resemble those found, for instance, in the Diptera.

The features characterising *Ornithogalum caudatum* are common to many other plants. The lists given by Lawrence (1931) and Darlington (1937) show that a great number of plants with small chromosomes exhibit secondary pairing in meiosis. In *O. caudatum* the seven large bivalents do not show any attraction, while the twenty smaller ones are associated in pairs. This may be interpreted in either of two ways. The seven large bivalents may actually be unrelated, while doublings have occurred among the smaller chromosomes, leading to the formation of the chromosome complement of *O. caudatum*. Or some of the larger chromosomes are related, but their size prevents any secondary association. A comparative study of the genus would throw light on this point.

The somatic attraction shown by the chromosomes in *O. graminifolium* is even stronger than in *O. caudatum*. Consequently the chromosome behaviour also deviates more from the normal. On the hypothesis developed above it would be supposed that the somatic attraction in this case too, depends on a slight degree of precocity in the external mechanism of the cell. The occurrence of chromatid bridges in the mitotic anaphases also fits in well with this line of thought. If the chromosomes are not completely divided, *i.e.* functionally double, when the anaphase separation begins, the formation of chromatid bridges is only to be expected (*cf.* Darlington and La Cour, 1940).

It has been pointed out by Oksala (1943) that the variable behaviour of univalents at meiosis in different organisms—especially their division in the first or second division respectively—must depend on the degree of precocity characterising the meiosis in each individual case. If the external changes in the cell are only slightly advanced,

the univalents have time to divide during the first division. If, on the other hand, precocity is strong, their division is postponed to the second division.

The precocity of the external changes which is present in the mitotic divisions of *O. graminifolium* is naturally even more pronounced in its meiosis. A number of chromosomes which obviously have been paired in pachytene, later fall apart owing to lack of chiasmata. In diakinesis the chromosomes which have remained as univalents repel each other as do the bivalents. In prometaphase the repulsion lapses and the chromosomes come together on the metaphase plate. Now if we suppose that the precocity is strong, the univalents are not yet functionally double and the chromosomes attract each other, pairing somatically. The fact that the univalents never divide during the first division is in accordance with this interpretation.

The various chromosomes in a single cell often represent different stages of the developmental cycle, and the anaphase separation does not take place simultaneously in the different chromosome pairs. Considering the deviations from normal meiosis found in *O. graminifolium*, its ultimate results are remarkably regular. As in the Diptera, somatic attraction has enabled the development of a new type of meiosis which, in its effects, however, resembles normal meiosis.

It must be noticed that in the present case there is no greater tendency to remain as univalents shown by either the larger or the smaller chromosomes. This again ensures that the genetic variation which is brought about by crossing-over is maintained in regard to all the chromosome types.

A case which in certain of its features resembles *Ornithogalum* has been described by Ribbands (1937) in a *Lilium* hybrid. In this plant too, a variable number of chromosomes which have paired in pachytene fall apart later owing to a failure of chiasma formation. In diakinesis they repel each other only slightly, retaining a clear "position correlation." In metaphase even this slight repulsion is overcome and the homologous chromosomes pair somatically, and subsequently separate. In consequence the homologous chromosomes occupy a correlated position on the spindle during the whole first division. At late metaphase a number of the univalents return to the plate and divide.

Somatic and secondary pairing have generally been interpreted as expressions of the homology of the chromosomes concerned. The homology may be more or less pronounced, even ancient relationships of the chromosomes coming to light in this way. Another explanation has been advanced by Thomas and Revell (1946) in regard to secondary pairing of bivalents observed in *Cicer arietinum*. In this plant secondary association between the eight bivalents does not show any specificity. In an autotetraploid derivative, however, the association seems to be preferential between homologous bivalents. Thomas and Revell assume that secondary association in this case

has originated from a fusion of heterochromatic chromosomes regions in pachytene, which continues through the intervening stages into metaphase.

This explanation does not seem to hold in the case of *Ornithogalum*. It is true that both the species now examined possess well-developed chromocentres. These do not, however, show any tendency to fuse either in mitosis or in meiosis. On the contrary, the heterochromatic bodies seem to be more condensed than the other chromosome regions. It should be pointed out that the heterochromatic bodies, in the pachytene of *O. caudatum*, for instance, are remarkably constant in number, no variation which could be interpreted as due to fusion being observable. In *Ornithogalum* the attraction of the chromosomes, both somatic and secondary, is quite obviously between homologous chromosomes. The units which show these kinds of association are similar in size and shape. A further fact corroborating the older view concerning secondary association is that in *O. caudatum* the chromosomes do not show any association in diakinesis, this feature becoming apparent only at metaphase. Since little attention has been paid to possible fusion of heterochromatic chromosome regions it is uncertain which interpretation applies to secondary association in other organisms in which it has been reported to occur.

5. SUMMARY

1. The chromosome behaviour of two *Ornithogalum* species, *O. graminifolium* ($2n = 10$) and *O. caudatum* ($2n = 54$), has been studied both in mitosis and meiosis. The characteristic feature of both these species is a strong tendency to somatic and secondary attraction, which is obviously an expression of the homology of the chromosomes concerned.

2. In *O. caudatum* a variable number of the smaller chromosomes lie in pairs in the mitotic metaphase plates. In the first division metaphase the twenty smaller bivalents are situated in twos, while the seven larger bivalents are spaced at random. A similar association is revealed by the chromosomes in second division metaphase plates. The course of meiosis is fairly regular.

3. In *O. graminifolium* the somatic attraction of the chromosomes, as seen especially in the mitotic metaphases, is even more pronounced than in *O. caudatum*. In meiosis the same tendency is reflected by the behaviour of the univalent chromosomes. In many cells a number of chromosomes which have been paired in pachytene fall apart owing to absence of chiasmata. They repel each other in diakinesis, but come together and pair somatically on the first division metaphase plate. Univalents never divide during the first division.

4. The somatically paired univalents in *O. graminifolium* are, as a rule, co-orientated on the metaphase plate. In a few cells, however, they show auto-orientation. In the former case a normal segregation takes place. Meiosis in this plant, though deviating from the normal,

is remarkably regular in its ultimate results. It thus bears a resemblance to certain exceptional modes of meiosis found in the Diptera, whose chromosome behaviour too is determined by the property of somatic pairing.

5. Chromosome conjugation in meiosis is brought about by the attraction of homologous chromosomes which are single. It has been supposed that for somatic and secondary attraction of the chromosomes a so-called residual attraction is responsible. These two attractions may be brought into relation with each other as follows. In accordance with the precocity theory of meiosis residual attraction may be thought to be due to the fact that the external changes in the cell are more or less precocious relative to those internal to the chromosomes. This, in turn, leads to the chromosomes being more or less *functionally single* at stages when in other organisms they are double. This state of affairs again accounts for the occurrence of residual attraction between the chromosomes. The degree of chromosome association is determined by two factors: the degree of doubleness of the chromosomes, which is at a maximum in metaphase, and the diminishing body repulsion of the chromosomes when prophase or diakinesis is succeeded by metaphase.

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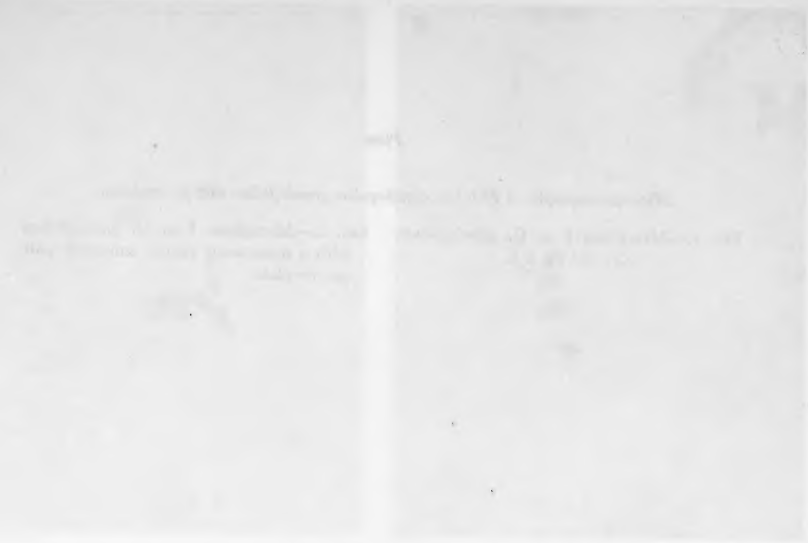


Plate

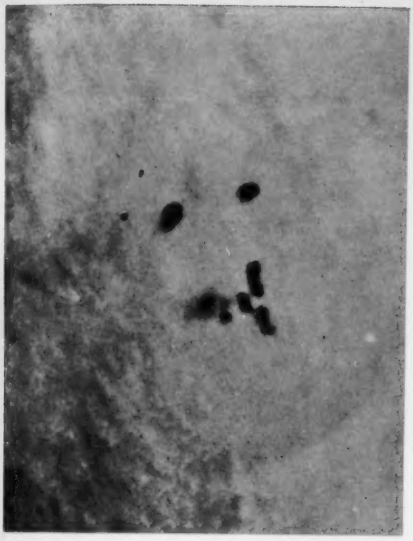
Microphotographs of PMC in *Ornithogalum graminifolium* and *O. caudatum*.

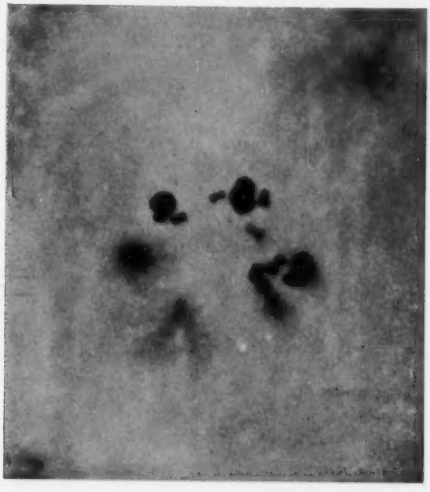
FIG. 1.—Metaphase I in *O. graminifolium*. *Cf.* text fig. 2 *f*.

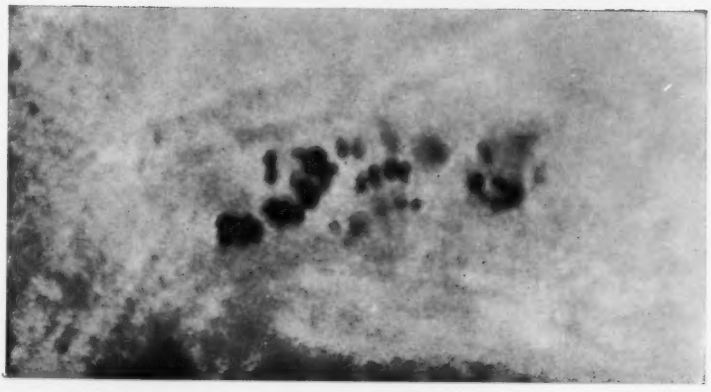
FIG. 2.—Metaphase I in *O. graminifolium* with a somatically paired univalent pair on the plate.

FIG. 3.—Metaphase I in *O. caudatum*; the small bivalents show secondary association. *Cf.* text fig. 4 *g*.

FIG. 4.—Side view of metaphase I in *O. caudatum*; secondary association of the smaller bivalents. *Cf.* text fig. 4 *e*.







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THE TAXONOMIC DISCRIMINATION OF BEES

A. J. BATEMAN

The John Innes Horticultural Institution, Bayfordbury, Herts

Received 29.xii.50

It has been known at least since Aristotle and repeatedly confirmed (see Grant, 1950) that hive bees tend to work one plant species at a time. This is in the interest of both plants and insects. For the plants it saves indiscriminant dissipation of pollen as in wind-pollinated species. For the insects their efficiency in the collection of nectar or pollen is doubtlessly increased if the manner of visiting flowers is standardised over long periods and the insect has not to be continually learning the best approach to a new species.

As a result of this relationship between plant and pollinator, differences in flower colour and form which are discernible to bees can play an important role in isolation between incipient species which as yet have no barriers to crossability other than the behaviour of their pollinators. The evolutionary significance of this relationship has been discussed by Grant (1949). Mather (1947) has argued that there will be a range of similarity between forms at and below the specific levels, over which the discrimination by the bees is absent or imperfectly developed. Under these conditions the degree of constancy of bees would be measurable by appropriate techniques.

It was to study this transitional phase in bee behaviour that the experiments about to be described were undertaken.

THE EXPERIMENT

Brassica napus (swede) is an allotetraploid hybrid between *B. oleracea* (cabbage) and *B. campestris* (turnip). Some of the main distinguishing features of the species are as follows :—

	B. oleracea	× *B. campestris*	⟶ *B. napus*
	n = 9	n = 10	n = 19
flowers	large	small	intermediate
pedicels	stout	slender	intermediate
corolla	pale yellow	bright yellow	bright yellow (type)
Varieties used—			
Green : aerial parts (excl. corolla) green			White-fleshed : bright yellow corolla
Red : aerial parts (excl. corolla) suffused with anthocyanin			Yellow-fleshed : dull yellow corolla

As has been previously observed (Bateman, 1947) bumble bees, which pollinate *B. oleracea* freely, never visit *B. campestris*. It was

inferred that the small flowers and pedicels of *B. campestris* caused bumble bees to avoid this species. The red colour in red cabbage is noticeably present even in the calyx, filaments and ovary. The particular green cabbage used had shorter plants at flowering time than the other three forms.

The experimental material consisted of 60 plants blooming in May 1949 and comprising 15 plants of each of the four types : red cabbage, green cabbage, yellow-fleshed swede and white-fleshed swede, arranged in random order. The activity of pollinating insects on this plot was observed on three days in May, the 4th, 6th and 13th. While several species of bee were observed on the plot they were classified into three classes only ; bumble bee, hive bee and solitary bee. The total amount of data did not warrant any further subdivision.

A bee leaving a flower on a given plant is more likely to visit next another on the same plant than one on any other (*ibid.*). In an experiment such as the present, therefore, the only relevant observations are the plants which the bees visit on leaving one plant for another. It is only then that they are presented with a choice between forms.

While the main experiment was in progress, a short distance away were two larger plots in full bloom side by side, one of swede and one of cabbage. A survey of the insects visiting these plots gave the following figures.

	Hive bees	Bumble bees	Solitary bees
Swede . . .	68	0	4
Cabbage . .	69	6	6

This gives the relative frequency of the three classes. The absence of bumble bees from the swede was confirmed by the detailed observations on the randomised plot. These are summarised in table 1.

INTERPRETATION

These observations are concerned with the discrimination of bees between plant forms. Such discrimination expresses itself in two ways. In the first way it appears as a preference for one of two forms when given free choice. It is not so easy, however, to measure such preference directly, because one can never be sure that there is equal freedom of choice between the species. Although the four varieties of *Brassica* used in this experiment were equally numerous, they varied in flower production. The green cabbage was definitely the least prolific in flowers and the swede varieties were most prolific.

Factors such as these, masking preference for a particular species

should, however, be the same for all insects. If we compare the distribution in *a*, *b* and *c* of table 1 it is evident that if we take hive bees as the norm (which does not imply that they show no preference),

TABLE 1

Pairs of consecutive plants visited classified by variety or species. Rows, first plant of the pair; columns, second plant of the pair. R G, Y W, C S represent red and green cabbage, yellow and white swede, cabbage and swede in that order

Pollinator	Hive bees	Bumble bees	Solitary bees
No. of forages	26	12	8
Total plants	301	98	53

	R	G	Y	W
R	55	6	6	3
G	9	17	0	6
Y	4	0	51	33
W	5	5	29	72

	R	G	Y	W
R	72	8	0	0
G	12	6	0	0
Y	0	0	0	0
W	0	0	0	0

	R	G	Y	W
R	1	0	0	3
G	1	0	0	1
Y	0	0	7	7
W	1	2	7	23

	C	S
C	87	15
S	14	185

(*a*)

	C	S
C	98	0
S	0	0

(*b*)

	C	S
C	2	4
S	3	44

(*c*)

bumble bees visit only cabbage and solitary bees show a strong preference for swede. Flower size may well be the deciding factor, since hive bees are intermediate in size between bumble bees and solitary bees. The discrimination against both swedes and turnips by bumble bees is indeed very strong, for in much bee watching on these crops I have never seen a bumble bee on either species.

The second way in which discrimination between forms can be expressed is in flower constancy. This appears to be a basic instinct in bees, extending over all insect-pollinated flowering plants. It may not be determined directly by the ability of the bee to discern any difference between types, though the failure to detect constancy in respect of flower colour alone (*e.g.* Mather 1947) could be due to insufficiently sensitive tests. The bee may well give varying weight to different characters producing a sort of "discriminant function" by which its behaviour is determined.

Flower constancy is measured by observing the frequency with which a bee leaving a plant of class A and given an equal choice of classes A and B, continues to visit A. If the bee visits A and B with equal frequency the flower constancy is zero. If it visits A only the flower constancy is at a maximum, say unity. We have, therefore, to derive a measure of constancy which varies from 0-1. In practice,

however, the insect is not given an equal choice. Firstly, an insect leaving a plant of variety A has a choice of 14 other plants of variety A to 15 plants of any other variety. The bias introduced in this way is trivial in comparison with the error variation and in any case is bias in the safe direction, that is it reduces the apparent discrimination. Secondly, the varieties vary in their abundance of flowers as mentioned above. Finally, there is the above-mentioned preference from whose effect our index of constancy must if possible be kept free. In calculating the index of constancy we must therefore allow for the different frequencies in the two like-to-like classes of each 2×2 table. A similar problem is presented in calculations using linkage data in which both pairs of alleles have differential viability, and has been dealt with mathematically in general form by Fisher and Bailey (1949). The constancy data present a particularly simple case. If we represent our 2×2 table as follows :—

		2nd visit: A	2nd visit: B
1st visit	A	a_1	a_2
1st visit	B	a_3	a_4

with $a_1+a_2+a_3+a_4 = n$

Then the best estimate,* or index, of constancy is

$$\frac{(a_1a_4)^{\frac{1}{2}} - (a_2a_3)^{\frac{1}{2}}}{(a_1a_4)^{\frac{1}{2}} + (a_2a_3)^{\frac{1}{2}}}$$

The test of significance of deviation of this expression from zero is given by the contingency χ^2 for one degree of freedom.

In this way we can calculate from the data in table 1A that the constancy of hive bees in respect of the species cabbage and swede is 0·795 with a χ^2 of 185·24. It remains a possibility that a spurious constancy could be obtained, if during the period of the observations the flowering of the two species was staggered, one species predominating at first and the other later. This is easily checked by taking the data for the three days separately as in table 2. There is highly significant constancy on each day.

* Bailey's estimate of the recombination fraction p from backcross linkage data, in our symbolism, is

$$\frac{(a_2a_3)^{\frac{1}{2}}}{(a_1a_4)^{\frac{1}{2}} + (a_2a_3)^{\frac{1}{2}}}$$

and varies from 0 when linkage is complete to $\frac{1}{2}$ with no linkage. For our present use we require an expression that is 0 when $p = \frac{1}{2}$ (no constancy) and 1 when $p = 0$ (complete constancy). The index of constancy given here is a derivative of Bailey's formula with the required properties.

In spite of the strong avoidance of cabbage by solitary bees it is still possible to calculate their specific constancy. It is 0·457 with a χ^2 of 4·52 (P = 0·04). It may at first seem surprising that the

TABLE 2

Hive bee data presented separately for each day's observations

Date in May	4th		6th		15th	
	C	S	C	S	C	S
C	34	12	6	1	47	2
S	12	124	0	22	2	39
$\chi^2_{[1]}$	77·11		23·78		74·60	

constancy is less than for hive bees which show much less preference. The above index takes into account, however, not only the fidelity to swede of insects pollinating swede but the fidelity to cabbage of insects pollinating cabbage. If solitary bees avoid cabbage even when they have just been pollinating it they will thereby lower their index of constancy.

Analysis of the data discloses discrimination also between varieties of the same species though rather weaker, as might be expected, than that between species. All calculable indices with their respective χ^2's are shown in table 3. The lower χ^2's for bumble and solitary bees

TABLE 3

Constancy indices for the three classes of bee for all visible comparisons

	Hive bees		Bumble bees		Solitary bees	
	Index	χ^2	Index	χ^2	Index	χ^2
C—S	0·795	185·24			0·457	4·52[2]
R—G	0·615	28·92	0·359	6·53[1]		
Y—W	0·325	19·14			0·289	3·13[3]

[1] P = 0·01 [2] P = 0·04 [3] P = 0·09

arise as much from the smaller numbers of observations as from the lower values of the index.

The discrimination between varieties is of some evolutionary significance since it shows how normal intra-specific variation can act as a stimulus to isolation by affecting bee behaviour. This in turn would increase the rate of divergence which would increase the bees' discriminatory powers. The lower constancy indices of bumble and solitary bees confirm observations of other workers (*vide* Grant, 1950).

One curious feature of the 4×4 table in table 1A is the apparently complete isolation between green cabbage and yellow swede. This may be a fortuitous result of the rather low numbers involved. (The

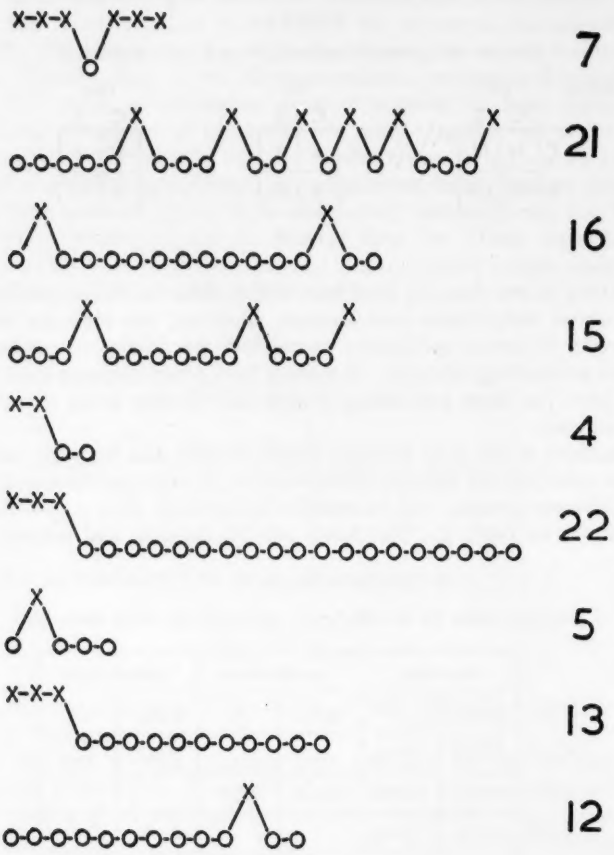

FIG.—Details of nine forages of hive bees visiting both species. *x* = a cabbage plant, *o* = a swede plant. Read from left to right. At extreme right is the total number of plants per forage. Besides those illustrated there were eight forages confined to cabbage, comprising :

4, 6, 7, 7, 10, 11, 19 and 22 plants

and nine forages confined to swede, comprising :

6, 7, 8, 10, 10, 14, 19, 22 and 30 plants.

frequencies of the comparable like×unlike crosses vary from 6 to 3.) On the other hand it may arise as an interaction between varietal characters. The green cabbage was distinct from the other three forms in plant height. The yellow swede was distinct from the rest

in flower colour. The two characters together might have reinforced the normal interspecific discrimination to give a greater discrimination than between any other pair of varieties.

Since the data were collected forage by forage it is possible to test for heterogeneity between forages (which is probably a measure of heterogeneity between bees) and to observe the precise sequence of visits in any one forage. Only the hive bee data are considered here since they were most extensive. Those forages involving crossing between species are presented in detail in fig. 1. Those confined to one species need be represented merely by the number of plants visited. The varieties have been ignored since they would have made the diagrams too complicated.

Owing to the variable sizes of the forages a statistical test of heterogeneity is out of the question. However some conclusions can be drawn from a superficial survey. Out of 26 forages, containing 29 instances of crossing from one species to another, an average of just over one per forage, 17 are confined to one species and only 9 are mixed. Of these 9, one, no larger than several pure forages, contains 11 crossings. Clearly there is heterogeneity between forages. This may be due to congenital differences in the bees, or to environmental factors such as age of the individual. By analogy with territorial fixation (Butler, 1945) it would appear possible that the more erratic forages are those of younger bees. In any case the immediate cause of inconstancy might be inadequate powers of discrimination.

Inspection of the mixed forages enables us to test this possibility. In all but three there is a tendency for the bee to pay most attention to one species, the visits to the second species being aberrations which are never continued for more than one plant at a time. This rather points to the lack of fixation being due to poorly developed powers of discrimination rather than indifference to which species is being worked. In the three exceptions apparently showing a switch in mid-forage from one species to the other the period on the first species is only two or three visits, possibly at the start of a forage, before the conditioned reflexes had got running smoothly. One minor feature of the data is that in all the mixed forages save one the main species is swede with aberrant visits to cabbage. In the three showing a switch, the switch is from cabbage to swede. This is very suggestive that the bees have a real preference for swede and it is only the strong species constancy of those bees working cabbage which keeps them on that species.

Tests have also been made for heterogeneity between forages in constancy to varieties. One might expect any such heterogeneity to be correlated with that found in specific constancy. If we calculate separately the constancy indices between swede varieties according to whether the bees show or do not show complete species constancy (data in table 4) we get very marked heterogeneity. Bees constant to swede have an intervarietal index of 0·402 and a χ^2 of 18·89.

Bees working both species have an index of only 1·135 with a non-significant χ^2 (1·06 = P of 0·3). Unfortunately a similar comparison

TABLE 4

Comparison of the constancy to swede varieties of hive bees grouped according to their species constancy

	Bees visiting swede only		Bees visiting both species	
	Y	W	Y	W
Y	41	18	10	15
W	17	41	12	31
Total plants	117		68	
χ^2	18·89		1·06 (P = 0·3)	
Index	0·402		0·135	

cannot be made using cabbage varieties because the bees working both species rarely worked two cabbage plants consecutively.

SUMMARY

Observations were made on bees foraging on a randomised plot consisting of equal numbers of two cabbage and two swede varieties.

Hive bees visit both species with about equal frequency, bumble bees visit only cabbage, while solitary bees concern themselves mainly with swede.

Hive bees show, at least within forages, a high but incomplete constancy to species and a lower but still highly significant constancy to varieties within a species. Wherever comparisons are possible the constancy of bumble bees and solitary bees is weaker than that of hive bees.

Examination of separate forages shows marked heterogeneity in degree of discrimination expressed both between species and between varieties. There is a correlation between interspecific and intervarietal discrimination.

Acknowledgments.—The author wishes to express his indebtedness to Miss Sheila Mann on whose bee-watching the entire paper is based.

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CHROMOSOME NUMBERS OF SUCCULENT PLANTS

BRIAN SNOAD
John Innes Horticultural Institution, Bayfordbury, Hertford, Herts

Received 31.i.51

THE following lists of chromosome numbers have been compiled from the collection of succulent plants established at the John Innes Horticultural Institution by G. D. Rowley, to whom I am grateful for help in the identification of certain species and for enlarging the collection for cytological studies.

The majority of observations were made from root-tip squashes pretreated with α-bromonaphthalene, fixed in acetic alcohol and stained in Feulgen, few flowers being available for the study of meiosis.

Two main groups were studied,

(*a*) *Aloinæ*—3 genera. (*b*) *Ficoidaceæ*—33 genera.

With one exception—noted below—the plants are all South African in distribution.

The basic number of the *Ficoidaceæ* is 9. The chromosomes are small and all with median centromeres, there being no differentiation of types.

The basic number of the *Aloinæ* is 7, and here there is far more differentiation between the chromosomes. They can be split up into four groups A, B, C and D as shown in fig. 1 (page 280).

There are slight differences between the karyotypes of the three genera—mainly differences involving the position of the satellites. When satellites are present in *Haworthia* they are similar in position to those in *Aloë*. Resende (1937), however, reported that the number of satellites is not constant for all the species in certain genera in the *Aloinæ*.

The degrees of polyploidy in both the *Aloinæ* and the *Ficoidaceæ* are summarised in table 1.

TABLE 1

	2x	3x	4x	5x	6x	7x	8x
Ficoidaceæ . . .	148 (51)	7 (4)	53 (12)	...	3 (2)	...	1 (1)
Aloë . . .	82 (15)	...	...	1 (...)	4 (4)	...	...
Gasteria . . .	23 (11)	1 (...)	3 (...)	...	...	...	...
Haworthia . . .	75 (35)	5 (2)	24 (5)	5 (2)	10 (3)	1 (...)	2 (1)
Total (*Aloë* excepted) .	246	13	80	5	13	1	3

(The numbers in brackets refer to the 148 individuals reported in the present list of chromosome numbers.)

It will be noticed that apart from *Aloë* the even-numbered species fall into geometrical progressions and the odd-numbered species may be regarded as a function of the numbers above and below each.

If these are a and b then the value $1/9\sqrt{ab}$ roughly fits. The odd numbers are therefore presumably hybrids between species above and below them in polyploidy.

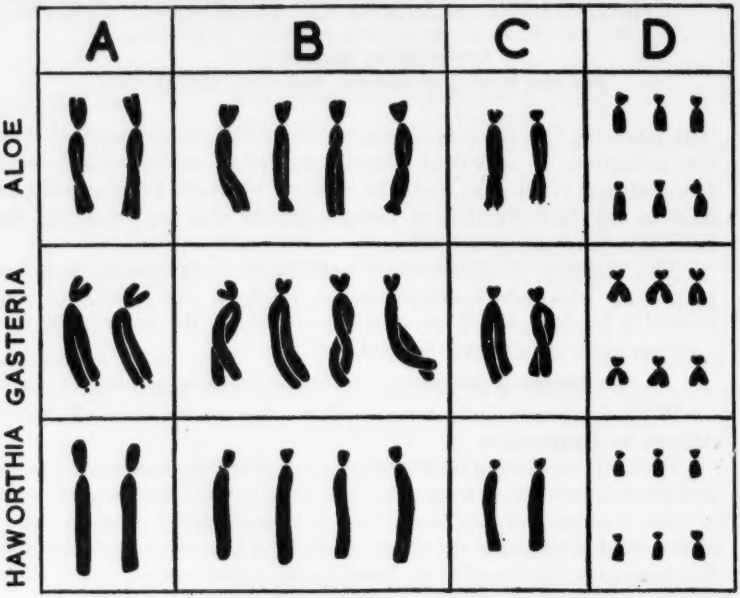

FIG.

In conclusion it should be pointed out that no "chromatic agglutination" as referred to by other workers (Resende, Rijo and Pinto-Lopes) was seen in any normal preparations of the *Aloinæ*. However, stickiness was easily induced by over-hydrolysis of the material prior to Feulgen staining and this may have been the cause of the trouble.

ALOINÆ: $x = 7$

ALOË	2x	6x
arborescens Miller		*ciliaris* Haw. (Edinburgh)
aristata Schult.		*ciliaris* Haw. (J. Brown)
brevifolia Miller		*ciliaris* Haw. (Monaco)
coccinea ?		*ciliaris* Haw. (V. Higgins †)
commixta Berger		*ciliaris* Haw., *tidmarshii* Schönl.
greenii Baker		*tenuifolia* Lam.
longifolia Haw.		*tenuior* Haw.
plicatilis Miller		
salaris Hort.		* Abyssinian.
saponaria Haw.		† Parent plant and 1950 seedling.
schimperi * Todaro		
sp. (J. Brown, Southall)		
spinosissima Hort.		
striatula Haw.		
variegata Linn.		

ALOINÆ—continued

GASTERIA 2*x*

armstrongii Schönl.
bayfieldii Baker
beckeri Schönl.
carinata Duval
colubrina N. E. Brown
croucheri Baker
lævis Haw.
liliputana v. Poelln.
pulchra Haw.
rurex Hort.
sp. Hort.

HAWORTHIA 2*x*

angusta ?
aristata Haw.
aspera Haw.
atrovirens Haw.
attenuata Haw.
beanii G. G. Smith
beanii G. G. Smith, *minor* G. G. S.
coarctata Haw.
correcta v. Poelln.
cuspidata Haw.
cymbiformis Duval
fulva G. G. S.
glabrata Baker
herrei v. Poelln.
herrei v. Poelln., *depauperata* v. Poelln.
hilliana v. Poelln.
icosiphylla Baker
krausiana ?
lepida G. G. S.
maughanii v. Poelln.
mucronata Haw., *polyphylla* ?
perplexa v. Poelln.
planifolia Haw.
pumila Duval
ramosa G. G. S.
reinwardtii Haw., *brevicula* G. G. S.
reinwardtii Haw., *grandicula* G. G. S.
reinwardtii Haw., *kaffirdriftensis*, G. G. S.
reinwardtii Haw., *riebeckensis* G. G. S.
subregularis Baker
syringoidea ?
tortuosa Haw., *var.*
truncata Schönl.
turgida Haw.
viscosa Haw.

3*x*

reinwardtii Haw., *chalumnensis* G. G. S.
reinwardtii Haw., *peddiensis* G. G. S.

4*x*

glauca Baker
greenii Baker, *silvicola* G. G. S.
reinwardtii Haw., *committeesensis*, G. G. S.
reinwardtii Haw., *huntsdriftensis* G. G. S.
reinwardtii Haw., *valida* G. G. S.

5*x*

rubrobrunea v. Poelln.
sampaiana Res., *brotereana* Res.

5*x*+1

sampaiana Res.

6*x*

coarctata Haw., v. *haworthii* Res.,
,, v. *kraussii* Res.
coarctatoides Res.

8*x*

tessellata Haw.

FICOIDACEÆ: *x* = 9

(i) 2*x* Genera

APTENIA
cordifolia Schwant.
ARGYRODERMA
ovale L. Bol.
ARIDARIA
canaliculata L. Bol.
tetragona L. Bol.
ASTRIDIA
maxima Schwant.
BIJLIA
cana N. E. Br.
CARPOBROTUS
edulis N. E. Br.
fourcadei L. Bol.
CARRUANTHUS
caninus Schwant.
CEROCHLAMYS
pachyphylla L. Bol.
CONICOSIA
capensis N. E. Br.
communis N. E. Br.
pugioniformis N. E. Br.

FICOIDACEÆ—continued

(i) *2x* Genera—*continued*

CORPUSCULARIA
lehmannii Schwant.
CYLINDROPHYLLUM
calamiforme Schwant.
DINTERANTHUS
microspermus Schwant.
ECHINUS
maximiliani N. E. Br.
EREPSIA
inclaudens N. E. Br.
HERERoA
incurva L. Bol.
stanfordiæ L. Bol.
NANANTHUS
aloides N. E. Br.
crassipes L. Bol.
ODONTOPHORUS
marlothii N. E. Br.
PLEIOSPILOS
prismaticus Schwant.
PRENIA
relaxata N. E. Br.
PSILOCAULON
granulicaule N. E. Br.
RHINEPHYLLUM
comptonii L. Bol.
STOMATIUM
conradii ?
paucidens L. Bol.
rosei ?

(ii) *4x* Genera

DROSANTHEMUM
candens Schwant.
HYMENOCYCLUS
purpureus Graessn.

(iii) Mixed Genera

BERGERANTHUS
artus L. Bol. . . . 18
multiceps Schwant. . . 18
scapiger N. E. Br. . . . 27
vespertinus Schwant. . . 36

CEPHALOPHYLLUM
acutum L. Bol. . . . 18
platycalyx L. Bol. . . . 36

CHEIRIDOPSIS
carnea N. E. Br. . . . 18
inspersa N. E. Br. . . . 18
meyeri N. E. Br. . . . 18
inæqualis L. Bol. . . . 27
bibracteata N. E. Br. . . 36
vanzijlii L. Bol. . . . 36

DELOSPERMA
aberdeenense L. Bol. . . 18
rogersii L. Bol. . . . 36

DISPHYMA
sp. II. 36
clavellatum? 54

FAUCARIA
brittenæ L. Bol. . . . 18
jamesii L. Bol. . . . 18
speciosa L. Bol. . . . 18
haageį Tisch. . . . 27

MESEMBRYANTHEMUM
aureum Linn. . . . 18
haworthii Don. . . . 18
incanescens 18
mallesoniæ L. Bol. . . . 18
productum Haw. . . . 18
roseum Willd. . . . 18
brownii Hook. f. . . . 27
glaucum Linn. . . . 36

RUSCHIA
impressa L. Bol. . . . 18
perfoliata Schwant. . . 18
piscadora Schwant. . . 18
rupicola L. Bol. . . . 18
karrachabensis L. Bol. . . 36
nonimpressa L. Bol. . . 36
uncinata Schwant. . . . 54

TRICHODIADEMA
stelligerum Schwant. . . 18
bulbosum Schwant. . . 36

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THE *Rh* ANTIGEN C^u

R. R. RACE and RUTH SANGER

Medical Research Council Blood Group Research Unit, Lister Institute, London

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THE *Rh* antigens c^v and C^u, allelomorphic to *C*, *c* and C^w, were described by Race, Sanger and Lawler (1948*a* and *b*). The description of C^u was notably incomplete; the donor could not be traced, and consequently the inheritance of the antigen could not at that time be demonstrated. Nevertheless, the sharp serological differences left no doubt that this new form of the *C* antigen must be due to an allelomorphic gene. It was estimated that the gene frequency of C^u is of the order of 0·2 per cent. in England. The antigen differed from the usual *C* in that the red cells carrying it were agglutinated by only two out of the six anti-*C* sera with which they were tested.

The C^u propositus has recently been traced and it has been possible to test the blood of his mother, the only relative available. By good fortune the mother not only has the antigen but has it in a combination in which it can be recognised, that is C^uc. The propositus is *O* and his mother A_1, otherwise their blood groups are the same, namely, C^uDe/cde, *MsNs*, *P*+, *Lu*(*a*−), *K*−, *Le*(*a*−) and *Fy* (*a*+).

The table shows the results of testing the blood of the propositus in 1947 and in 1950, and of his mother in 1950.

The two examples of C^uc cells were tested against titrations of the antisera shown in the table. No definite quantitative differences were revealed, for when C^u is agglutinated it usually scores as highly as *C*: moreover, our strongest anti-*C* serum (*Ba.*) is amongst those which fail to agglutinate C^uc cells.

The table also shows the reactions in albumin of two anti-*C* and two anti-C^w sera. These sera lacked incomplete anti-*D* and therefore could be used without the *D* reaction confusing the issue. Of these four sera, *Ma.* was the only one to give a positive antiglobulin test with C^uc and *Cc* cells; *Ed.* does not give a positive anti-globulin test with any *C* cells though the reaction is quite powerful in albumin.

Absorption tests showed that the cells of the propositus were able to remove anti-*C* from the serum *Ba.* (which does not agglutinate C^uc cells in saline) and from the sera *Hi.* and *Ed.* (which do agglutinate C^uc cells in saline). In no case was the absorption quite as efficient as that brought about by *Cc* cells. It was only possible to test the absorptive power of the cells of the mother against one serum, *Ba.* For some unexplained reason these cells were less efficient at removing anti-*C* than were the cells of her son and only slightly more efficient than the *cDe/cde* control cells.

TABLE

The reactions of the red cells of the C^w propositus and of his mother

Anti	In saline																In albumin			
	-D	*-E*	*-e*	*-c*	*-C^w (Lo)*	*-C^w (Du)*	*-C (Br)*	*-C (Ho)*	*-CC^w (Ba)*	*-CC^w (Ed)*	*-CC^w (Pe)*	*-CC^w (And)*	*-C (Pi)*	*-CC^w (Hi)*	*-C (Jo)*	inc. *-CC^w (Ma)*	inc. *-CC^w (Ma)*	*-CC^w (Ed)*	*-C^w (Lo)*	*-C^w (Du)*
The propositus *$C^w De/cde$* 1947 .	+	−	+	+	−	...	−	−	−	−	+	+	−	...	...	−	...	...	...	...
,, ,, 1950 .	+	−	+	+	−	−	...	−	−	−	+	+	−	+	−	−	+	+	−	−
His mother *$C^w De/cde$* 1950 . .	+	−	+	+	−	−	...	−	−	...	+	+	−	+	−	−	+	+	−	−
Controls *CDe/cde*	...	...	...	...	−	−	+	+	+	+	+	+	+	+	+	−	+	+	−	−
,, *$C^w De/cde$*	...	...	...	...	+	+	−	−	+	+	+	+	*w*	+	−	−	+	+	+	+
,, *cDe/cde*	...	...	...	...	−	−	−	−	−	−	*w*	−	−	−	−	−	−	−	−	−

inc = incomplete antibody
w = weakly positive reaction

Another serological problem arose when it was found that the *Ba.* serum which does not agglutinate C^uDe/cde cells in saline would do so after repeated absorption with *cDe/cde* cells ; this was not due to unmasking of anti-*D*, for *cDe/cde* cells were not agglutinated by the absorbed serum.

Unfortunately circumstances prevented either of these problems being pursued and this paper is therefore confined to the demonstration of the inheritance of the antigen C^u.

Acknowledgments.—We are greatly indebted to Dr W. Weiner, of the National Blood Transfusion Service, Birmingham, who traced the original C^u donor and obtained samples of blood from him and his mother.

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NEW ESTIMATES OF SOME RECOMBINATION FRACTIONS IN *ESCHERICHIA COLI*, ALLOWING FOR THE INFLUENCE OF DIFFERENTIAL VIABILITY

NORMAN T. J. BAILEY

Department of Medicine, University of Cambridge

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EXTENSIVE data on recombination in *Escherichia coli*, K—12 were given by Lederberg (1947, p. 514). Using a somewhat unsophisticated method of analysis he derived an approximate chromosome map (p. 516). Bailey (1951), illustrating a test for differential viability in bacterial genetics with a part of Lederberg's data, showed incidentally that the segregation of V_1^r/V_1^s was disturbed. It is therefore desirable to reassess the original data, making due allowance for differential viability effects.

The loci under consideration were shown by Lederberg to be arranged in the order shown in fig. 1.

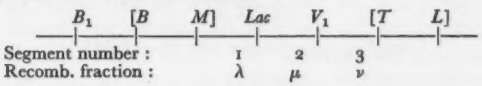


FIG. 1.

The symbols used for the various loci are as follows :—

Nutritional requirements

B_1 aneurin (thiamin)
B biotin
M methionine
T threonine
L leucine

\+ indicates independence
— indicates a requirement

Bacteriophage resistance

V_1 resistant to T1, T5
r indicates resistance
s indicates sensitivity

"Sugar" fermentation

Lac lactose

\+ indicates ability to ferment
— indicates inability

The actual order of the loci in brackets $[BM]$ and $[TL]$ is uncertain, and these combinations are regarded as single units.

So far as the biochemical markers are concerned all the crosses under discussion were of the type

$$B_1^-B^+M^+T^-L^- \times B_1^+B^-M^-T^+L^+$$

Prototrophs were recovered either from minimal media or from plates supplemented with aneurin. In the former case recombination was "compulsory" over both the segments B_1—$[BM]$ and $[BM]$—$[TL]$. In the latter case recombination was obligatory only over $[BM]$—$[TL]$, and was "free" over B_1—$[BM]$. The "free" recombination

fraction between B_1 and $[BM]$ is only of the order of 10 per cent. (Lederberg, 1947, p. 513) and it is proposed to examine both cases separately for evidence of interference.

As regards the other loci, *Lac* and V_1, Lederberg gave data on three of the four possible mating types. All the relevant material is summarised in tables 1 and 2. The numbers (1), (2), (3) and (123)

TABLE 1

Free recombination over B_1—[B M]

Mating types	Prototrophic types (recombinants) $B^+M^+T^+L^+(B_1^+$ or $B_1^-)$				
	(1)	(2)	(3)	(123)	Total
$B_1^-B^+M^+T^-L^-$ $B_1^+B^-M^-T^+L^+$					
$Lac^-V_1^s \times Lac^+V_1^r$ . .	159 (27·9)	244 (42·8)	157 (27·5)	10 (1·9)	570
$Lac^-V_1^r \times Lac^+V_1^s$ . .	80 (21·4)	151 (40·4)	134 (35·8)	9 (2·4)	374
$Lac^+V_1^s \times Lac^-V_1^r$ . .	102 (25·4)	201 (50·1)	91 (22·7)	7 (1·7)	401

TABLE 2

Compulsary recombination over B_1—[B M]

Mating types	Prototrophic types (recombinants) $B_1^+B^+M^+T^+L^+$				
	(1)	(2)	(3)	(123)	Total
$B_1^-B^+M^+T^-L^-$ $B_1^+B^-M^-T^+L^+$					
$Lac^-V_1^s \times Lac^+V_1^r$ . .	387 (29·4)	602 (45·8)	303 (23·1)	22 (1·7)	1314
$Lac^-V_1^r \times Lac^+V_1^s$ . .	61 (19·0)	145 (45·0)	107 (33·2)	9 (2·8)	322
$Lac^+V_1^s \times Lac^-V_1^r$ . .	28 (23·9)	46 (39·3)	37 (31·6)	6 (5·1)	117

refer to recombination over the first, second, third on all three of the segments shown in fig. 1. The figures shown in brackets are, of course, percentages. It should be observed that the figure of 303, appearing in column 3 for the first mating-type in table 2, was wrongly given in the original table as 203. The error was obvious on comparing the actual numbers with the percentages, and Lederberg (personal communication) tells me that 303 is correct.

The general procedure for estimating recombination fractions from this sort of data in the absence of interference was discussed by Bailey (1951). Similar methods can be used in the present instance, introducing additional parameters to represent viability effects. Let the

recombination fractions for the three sub-segments of the segment of compulsory recombination be λ, μ and ν as shown in fig. 1. Further, let the viability of *Lac*$^+$ relative to *Lac*$^-$ be u; and the viability of $V_1{}^s$ relative to $V_1{}^r$ be v; the two viabilities being assumed to operate independently. Then the expectations of the four kinds of prototrophs for the first mating-type in tables 1 and 2 are as shown in table 3.

TABLE 3

Expectations for first mating-type

Mating type	Prototrophic types (recombinants)			
	(1) *Lac*$^+V_1{}^r$	(2) *Lac*$^-V_1{}^r$	(3) *Lac*$^-V_1{}^s$	(123) *Lac*$^+V_1{}^s$
$B_1{}^-B^+M^+T^-L^-$; *Lac*$^-V_1{}^s$ × $B_1{}^+B^-M^-T^+L^+$; *Lac*$^+V_1{}^r$	$u\lambda(1-\mu)(1-\nu)$ $\times n_1/R_1$	$(1-\lambda)\mu(1-\nu)$ $\times n_1/R_1$	$v(1-\lambda)(1-\mu)\nu$ $\times n_1/R_1$	$uv\lambda\mu\nu$ $\times n_1/R_1$

n_1 is the total number of prototrophs from this type of mating and R_1 is given by

$$R_1 = u\lambda(1-\mu)(1-\nu)+(1-\lambda)\mu(1-\nu)+v(1-\lambda)(1-\mu)\nu+uv\lambda\mu\nu.$$

Similar expressions can be written down for the other mating types. This indication of the mathematical model adopted should be sufficient to show the assumptions made. It is unnecessary to reproduce here the computational details of the maximum likelihood scoring procedure which was carried out in the usual way. The results obtained were as follows.

Considering the data in table 1 first, we have the maximum likelihood estimates, with attached standard errors,

$$\left.\begin{array}{ll} \lambda_1 = 16{\cdot}28\pm1{\cdot}30 \text{ per cent.} & u_1 = 1{\cdot}038\pm0{\cdot}067 \\ \mu_1 = 25{\cdot}64\pm1{\cdot}61 \quad ,, & v_1 = 0{\cdot}775\pm0{\cdot}051 \\ \nu_1 = 19{\cdot}70\pm1{\cdot}36 \quad ,, & \end{array}\right\} \quad . \quad (1)$$

where the subscript 1 indicates results with free recombination over $B_1-[BM]$. On the basis of the values given in (1) we can calculate the expected numbers in the various classes and then derive a goodness-of-fit χ^2. We find $\chi^2_{(4)} = 5{\cdot}51$, based on four degrees of freedom; this is not significant and implies a satisfactory fit. The *Lac*$^+$/*Lac*$^-$ segregation is clearly undisturbed, but there is a deficit of $V_1{}^s$ organisms compared with $V_1{}^r$.

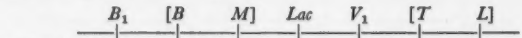
Similar calculations performed on the data of table 2 yield the results

$$\left.\begin{array}{ll} \lambda_2 = 17{\cdot}95\pm1{\cdot}89 \text{ per cent.} & u_2 = 1{\cdot}026\pm0{\cdot}104 \\ \mu_2 = 27{\cdot}11\pm1{\cdot}80 \quad ,, & v_2 = 0{\cdot}784\pm0{\cdot}051 \\ \nu_2 = 19{\cdot}53\pm1{\cdot}55 \quad ,, & \end{array}\right\} \quad . \quad (2)$$

where the subscript 2 indicates results with compulsory recombination over $B_1-[BM]$. This time the goodness of fit is not satisfactory with

$\chi^2_{(4)} = 15{\cdot}5$. In spite of this, however, it is remarkable that none of the estimates appearing in (2) is significantly different from the results obtained in (1). It is perhaps not unreasonable to conclude that the presence or absence of recombination over the segment $B_1-[BM]$ has a negligible effect on the degree of recombination observed over the segment $[BM]-[TL]$: for the loci represented in fig. 1 there is, *on the data available*, no evidence of interference.

Owing to the poor fit of the results in (2) we are hardly justified in pooling the information in (1) and (2). The recombination fractions and corresponding map distances (derived from Haldane's formula) for the segment $[BM]-[TL]$ are shown in fig. 2 for the case of free recombination over $B_1-[BM]$.



Recomb. fraction (per cent.)	16·3	25·6	19·7
Map distance (cM)	19·7	35·9	25·0

FIG. 2.—Chromosome map of *Escherichia coli*.

Comparing the *map distances* in fig. 2 with the corresponding values given by Lederberg (1947, p. 516), *i.e.* 22, 38 and 20, we see that the latter values were not entirely satisfactory, the estimate for $V_1-[TL]$ being particularly affected by disturbance due to differential viability. Of course it should be mentioned that if there is appreciable interference—of Kosambi type, for example—then the map distances in fig. 2 will all have been seriously underestimated.

Acknowledgment.—I would like to express my thanks to Miss Eva Rowland for her assistance with the computations on which the results of this paper are based.

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REVIEWS

POPULATION GENETICS AND ANIMAL IMPROVEMENT. By I. M. Lerner. Cambridge Univ. Press, 1950. Pp. 342+xviii. 30s.

The author commences his preface with the statement that " The purpose of this book is to raise rather than to answer questions," and indeed it is not easy to see what other course is open ; for the subject of population genetics, in the sense that Dr Lerner uses the term, is full of unanswered questions, questions that only extensive experimentation can answer. They will be answered adequately and economically, however, only if they are posed correctly ; and they can be posed correctly only if the genetical principles at issue are made clear and the available information weighed and carefully sifted for pointers. This Lerner sets out to do, and, in the present reviewer's opinion, succeeds to a very great extent in accomplishing.

Dr Lerner has been associated since 1933 with the project for raising the egg production of the University of California flock of Single Comb White Leghorns by a systematic programme of selection. It is therefore with poultry breeding that he is chiefly concerned, and from poultry breeding, especially the breeding of the University of California flock, that he draws most of his experimental evidence. He devotes three chapters to the history of attempts to improve egg production by genetic manipulation, to the nature and components of the production index by which he measures egg production, and to an account of the University of California flock. These chapters will be of value in their own right to the poultry breeder, and indeed to all who have an interest (no matter how academic) in animal production. Their chief function, however, is to give the background against which the essential genetical principles of animal breeding are discussed in the remaining eleven chapters. They point the need for the genetical discussion and in some measure they determine the course which it will follow.

The primary genetical postulate, or limiting condition of the discussion as the author calls it, is that " characters of economic importance depend on large numbers of genes, whose individual effects cannot ordinarily be isolated." While, as the author points out, some economically important variation is of a simpler genetic nature, few with experience in plant and animal breeding will dispute the general truth of this primary postulate. This leads directly to Lerner's great point of emphasis, viz. that if the variation to be manipulated is polygenic, the methods to be used must be those appropriate to polygenic systems. The mendelian techniques of analysis and prediction, developed for and appropriate to discontinuous variation, fail when the variation becomes continuous. A polygenic approach is needed, with corresponding genetical theory and statistical technique.

The essential genetical principles are listed in chapter five. Then in the next eight chapters they are taken up one by one and discussed in detail, in the light of the available evidence (especially that from poultry) and in relation to methods of application. After a further chapter on

miscellaneous questions, the book concludes with a statement of the many questions upon which our knowledge is inadequate and which require experimental investigation.

In his statement of the principles involved, of their operation in practice, and of the genetical information which experiment must seek to provide, Lerner is clearly speaking from long and mature reflection. Much of what he has to say is perhaps common ground to all who are interested in this branch of genetics. The statement is, however, so scholarly, so comprehensive and so well balanced as surely to command respect from all who read it. Few will fail to find something new in treatment or emphasis, and the reader to whom this field is unfamiliar will have an admirable introduction to the principles and questions at issue.

It is, of course, impossible to discuss the principles and experimental needs without reference to methods of analysis. These are necessarily of a biometrical and statistical nature and require some mathematical facility for their understanding. Lerner has omitted from his account the derivation of the formulæ which he uses, as being extraneous to his chief purpose and in order to keep the book within manageable length. He includes, however, full references to the original sources and also a glossary of the many symbols which are used. The formulæ and methods are taken from Wright's original writings on the subject via the adaptation and elaboration of Lush and his school. Thus this part of the book is less particularly Lerner's own, and, to this reviewer at least, is less satisfying because more circumscribed than the parts for which Lerner can be held more specifically responsible.

Certain basic expressions will be generally agreed as common ground, since they are in essence the mathematical formulations of agreed genetical statements. We may, however, observe in passing that the notation in which these are expressed is not as clear as it could be made. Thus on page 84 we find the expression

$$\sigma^2_{G_e} = \sigma^2_G + \sigma^2_{G'}$$

indicating that the genetical variance ($\sigma^2_{G_e}$) is regardable as composed of two parts, the additive (σ^2_G) and the non-additive ($\sigma^2_{G'}$), which latter depends on dominance, epistasis, etc. Now the distinctive features of these three terms are to be found not even in the subscripts, but in the sub-subscripts (or lack of them). The implication of the expression is thus largely concealed from all but the closest scrutiny. Surely we may take it that having agreed to discuss variances and in particular genetic variances, we need not make the expression say all this again, but allow it to concentrate on its own task of clearly setting out the relations of the various types of genetic variance, by taking the σ^2_G for granted and writing, *e.g.* something like $G = A+N$ or (in a notation which I have used elsewhere) $G = D+H$.

This kind of criticism can be levelled at much of the notation. It is in a sense a trivial point. Clear notation can, nevertheless, be of great help not only to the reader, but also to the investigator concerned to manipulate the expressions, both in saving time and in avoiding misapprehension and mistakes.

The chief criticism, or perhaps limitation would be a better word, of this mathematical approach springs, however, not so much from the way it is set down as from what it seeks to do. Any algebraic formulation must,

to be useful, be over-simple. Genes have too many properties of action and interaction for them all to be set out usefully in the formulæ we use. The system Lerner follows recognises this and deliberately concentrates (as most of us would) on the additive portion of the genetical variance. This course of action can, however, be misleading and there is obvious need for experimental work to test its validity or at least its utility—as indeed Lerner points out in his last chapter. In the absence of such information, which is gradually coming to hand for some species, even if for none that Lerner discusses, it is surely necessary to make provision in the mathematical formulation for a measure of the uncertainty in calculation and prediction to which the possible falsity of this simplifying assumption gives rise. The elaborate formulæ which are necessary for the interpretation of polygenic behaviour in stock animals can be no more reliable than the quantities which they combine and manipulate. To say that the experimental work necessary to give these measures of uncertainty cannot be carried out in large animals is merely to say that our large animal programmes need underpinning by experimental work with more readily handlable species. Again we feel that Lerner would agree—indeed some of the experimental designs he describes will give this type of information ; but the mathematical formulation he uses does not fully bring out the need for measures of uncertainty.

There are two basic quantities in all this mathematical elaboration, the heritability, as it is called, and the inbreeding coefficient. The measure of heritability must in general reflect departures from additive gene action, and if these are unknown must be treated with corresponding caution : and obviously so must any calculation based on it. The heritability has another limitation. It is essentially the ratio of the heritable to the total variation. It will therefore vary with changes both in genetical constitution and in environment. If, however, we seek to measure and use the heritable and the non-heritable variation as separate quantities, rather than relying on their ratio, we can go further towards understanding just what is changing the heritability of the character ; so that there is more chance of order coming out of what might be apparent chaos.

The inbreeding coefficient is suspect in another way. It is computed assuming uncomplicated Mendelian inheritance of the operative genes. But we have reason to believe, for example, that heterozygotes will enjoy an advantage over homozygotes in many species. In such a case the inbreeding coefficient as commonly computed must overestimate the actual effect of inbreeding. We need experimental evidence of just what does in fact go on. In the meantime major calculations derived from the inbreeding coefficient must be suspect, and minor corrections for it hardly worth the work of calculation.

All this is not to say that the sort of calculation Lerner describes is unnecessary. On the contrary it is essential to our understanding of those populations of domestic animals that we call flocks, herds and breeds. But our prime need now is for genetical experiments to test the assumptions on which these calculations are based and to measure the uncertainty which is inherent in them. The pleasure which many of us (including myself) get from the algebraic reduction of a complex problem must not blind us to this primary need of detailed, extensive and relatively tedious experimentation.

These considerations are clearly well to the fore in Lerner's mind, as any careful reader of his text will see. They are reiterated now with the sole purpose of emphasising that his text must be read and not merely the algebra enjoyed. One further point requires a little comment. It is assumed all through that the operative genetic system contains many genes, and that we can assume many units of segregation. This is doubtless well justified in domestic animals whose chromosome numbers are large. In species with lower numbers of chromosomes there also may well be many genes in the system ; but they appear often to segregate in a relatively small number of composite temporary units which I have called effective factors. In such cases the assumption of a large number of independently inherited genes could lead to error, especially in predicting behaviour under selection.

This having been said, the book can be heartily recommended to all serious students of production genetics, not only of animals but of plants too. For the plant breeder's problems, though differing in detail, arise from the same genic behaviour and involve the same essential principles.

Perhaps before concluding I may be permitted two minor personal comments, since they concern points on which Lerner specifically differs from me. He prefers the term " Population Genetics " to my " Biometrical Genetics." True, the problems he discusses are those of populations, though population genetics does not end with the study of polygenic variation. But, as we have seen, the study of polygenic variation must bring in controlled crossing experimentation more akin to the practical methodology of mendelian experiments than to the study and manipulation of populations of unknown genetic structure. The special feature of the work, whether on populations or on the offspring of controlled crosses, is that it is concerned primarily with continuous variation and therefore requires a biometrical rather than a mendelian analysis. So, as a general description, I still prefer Biometrical Genetics. And surely we have passed the time when the term biometry can fairly be regarded as having a dangerous anti-genetical flavour.

Secondly, in emphasising the polygenic point of view, Lerner expresses his feeling that I have been over-conservative in labouring its relation to mendelian genetics. Biometrical genetics would, however, be impossible if we could not start with the knowledge that the genes with which we must deal are transmitted exactly as are the major genes of mendelian genetics. Mendelian genetics is our sure and only foundation. Without it we should be no more able than Galton to make sense of continuous variation. As such it is worth a little acknowledgment, especially in an exposition of the methodology which our studies of polygenic variation entails.

These two points of difference are obviously minor ones. Lerner and I work with different characters in different species, but out problems are basically the same and we approach them with the same point of view. Our agrement is great and our difference small. *Population Genetics and Animal Improvement* has given me a double pleasure, of heartily recommending it as well as of profitably reading it. K. MATHER.

THE EVOLUTION OF *GOSSYPIUM* and the Differentiation of the Cultivated Cottons By J. B. Hutchinson, R. A. Silow and S. G. Stephens. Oxford University Press, 1947 Pp. xi+160. 15s.

The intensive genetical investigation of cotton and its wild relatives has advanced knowledge of the interrelations of the species and their evolutionary history to a higher level than that in any comparable group of plants. The present monograph consists of four essays on aspects of the evolution of *Gossypium* written by three well-known cotton geneticists as the Final Report of the Genetics Department of the Cotton Research Station, lately in Trinidad.

The first part is a revision by Dr Hutchinson of the classification of the genus, which he divides into twenty species grouped into eight sections. The sections generally have different geographical distributions and are construed with full regard to the facts of cytogenetic analysis. Six of the sections include all the wild species which are diploid ; one section is Australian, three New World and two African and Arabian. The seventh section includes the Old World diploid cultivated cottons, the eighth the New World tetraploid cultivated cottons together with one tetraploid wild species from Hawaii.

In the second part, Drs Hutchinson and Stephens consider the major factors which governed the evolution of the commercial cottons from the wild, often virtually lintless species. The relations of the wild species are first discussed, adopting the late Dr J. O. Beasley's genome nomenclature, which recognises five differentiated sets of chromosomes, A to E, in the genus. Set A is typified by the Old World cultivated diploids, B by the African *G. anomalum*, C by the Australian *G. sturtii*, D by the American wild species and E by *G. Stocksii* from the Sind and Arabia. Evidence is advanced for the view that the separation of the progenitors of these groups was very ancient, probably Cretaceous.

All species of *Gossypium* have at least some seed hairs, in whose development there is a continuous deposit of cellulose until at maturity the central cavity is almost obliterated. In lint hairs the cellulose deposit is much less, and the hairs collapse and twist on drying. The twists and convolutions give cotton the clinging property that makes spinning possible. There is evidence of the possibility of the origin of lint from normal hairs by mutation. The most ancient cotton fabrics known are fragments from Mohenjo-Daro in Sind dated at about 3000 B.C. and there is other evidence which points to the Indus Valley as the original home of cotton cultivation. The subsequent differentiation of the Old World cottons are considered in the third part by Drs Hutchinson and Silow.

The New World cultivated cottons present a specially interesting problem. Cytological analysis of these tetraploids shows that they are allopolyploids with A and D sets of chromosomes. The homology of the D set of the New World cottons is much closer to that of the Peruvian *G. raimondii* than to any other wild American species. The problem is how the A and D diploids were brought together. The A and D diploids occur on the tropical borders of the Pacific, while the AD tetraploids have their major centres of variability near the Pacific coasts of America, within the area occupied by the D diploids and otherwise are endemic in Pacific islands.

The migration, it is believed, was of the aggressive diploid A species and trans-Pacific rather than trans-Atlantic, on the grounds of the distribu-

tions of the New World species and the more ancient occupation by diploid cottons of southern Asia than of Africa. Professor Harland's theory of migration across a Pacific landbridge in late Cretaceous or early Tertiary times is rejected. Moreover, the cytogenetic data justify the assumption of a much more recent origin of allopolyploidy and a relatively close homology between the allopolyploids, all of which are linted, and their nearest diploid relatives. A recent origin excludes natural spread, and the theory is advanced that man carried the diploid cultivated cottons across the Pacific. The cytogenetic evidence demands only one origin of allopolyploidy, while the botanical evidence of the distribution of variability places the probable place in Northern Peru. The recent origin has, however, been challenged by Professor Stebbins, who considers the New World allotetraploids to have originated in the early Tertiary period. Moreover, it is surprising that if man indeed took linted cotton to the New World, that he failed to take also his main food plants.

The third section traces the differentiation of the true cottons, under domestication, by the selection of large seed, of copious, long and easily detachable lint and of extremes of white and brown colour. The eastward spread of *G. arboreum* is traced and likewise its westward diffusion from Sind, in the course of which *G. herbaceum* arose by selection. The collapse of the Indus civilisation about 2500 B.C. would have split *G. arboreum* into two areas, leading to genetic divergence and the establishment of specific differences. The details of the probable course of the later history cannot be adequately indicated in summary, but it forms a closely woven story in which botany and archæology provide mutual support.

The only linted Old World cotton that, from its distribution, could have been carried across the Pacific is *G. arboreum*. The three New World cultivated species have genetic isolation barriers between them, the more northerly *G. hirsutum* presumably having diverged from the southerly *G. barbadense* through a period of isolation following the introduction of cotton from South into Central America. The later differentiation and spread of the cultivated cottons in the New World is traced.

The final section by Drs Hutchinson and Stephens considers the significance of *Gossypium* in evolutionary studies. Firstly there is the evolution of new characters, for which lint hairs and annual habit provide models, and secondly the significance in evolution of polyploidy which is often associated with species differentiation in plants but rarely with the establishment of major evolutionary lines. The nature of genetic variability is discussed and attention is drawn to the desirability of its conservation as it may aid adaptation to varied local conditions. In the origin of discontinuity, the spread of cultivation may result in the development of special locally adapted types and, with the confluence of species already separated by genetic barriers built up in isolation, in the reinforcement of isolating mechanisms, as, for example, in the " corky " mechanism in the New World cottons.

The authors have done a signal service in demonstrating the wide interest and value, both academic and practical, of the results of the intensive genetic study of the cotton plant. The Empire Cotton Growing Corporation are to be congratulated on the vindication of their far-sighted policy of fundamental botanical and genetical studies, a policy which deserves to be extended to other crops and stocks. D. G. CATCHESIDE.

RACES. A Study of the Problems of Race Formation in Man. By C. S. Coon, Ph.D., S. M. Garn, Ph.D., and J. B. Birdsell, Ph.D. Pp. 164, 70 illustrations. Blackwell Sci. Publ. London. 21s. 6d.

In a study of human races our knowledge of genetics has to be applied to the understanding of variation in a species that cannot be bred experimentally. To meet the difficulty the available genetical technique and theory are, however, continually expanding. The study of the chromosomes, of disease resistance, of twin psychology, of blood group frequencies and even of language are providing new means of determining and describing the origin and character of the races of man.

The present book is an attempt to explain and define human races with the help of this new information. So far as it goes it is useful and sound. It is also sometimes vague and sometimes naïve. The genetics is that of Morgan, 1925, and it is interesting to see just how this genetics with its 44,000 genes sounds when it is applied to man at the present day. The main argument, however, is intended to show how various physical properties of the human races are adaptations to heat, cold, humidity, radiation and so on. The importance of disease resistance is not overlooked. But the distinction between linkage and correlation is not always certain to the writers. It is not surprising therefore that they do not understand the influence of the breeding system and the social customs underlying it and even sometimes seem to hesitate on the edge of Lamarckism. Towards the end of the book the classical " types " of 30 races are brought back on to the stage and the genetic scheme fades away into almost undiluted physical anthropology.

The authors frequently pause to ask why certain evolutionary changes have taken place in man and to tell us that they do not know the answer. Why are the Indonesians smaller than the Chinese? " Perhaps through selection. . . . Perhaps as a result of the new distribution. . . . Perhaps through mixture." If they had gone a little further into genetics and thought a little more about it they would then have been able to relate the beginning of the book to the end. Not only then would they have known the answers but they might also have been able to explain them to their readers.

C. D. DARLINGTON.

PLANT BREEDING. By Dr A. L. Hagedoorn. (Agricultural and Horticultural Series.) Pp. 237, 4 plates. London : Crosby Lockwood & Son, Ltd., 1950. 12s. 6d. net.

This is not claimed to be either a textbook on genetics or an exhaustive treatise on plant breeding. It is written for those " actively engaged in the amelioration of plants." Books synthesising plant breeding and genetics are welcome, providing they inject the scientific spirit into the age-old art of plant improvement. It is therefore all the sadder that unfortunately Dr Hagedoorn's synthesis is handicapped because it is often inaccurate, inadequate and out of date on plant genetics. For instance, it scorns the use of statistical analysis (a current " fashion ") and experimental design, while the colchicine technique for producing polyploidy is dismissed in three lines. Some of the literature recommended is in Dutch and useless for those likely to read the book ; the latest plant breeding reference is dated 1938. This book, which is written in a not unpleasing personal vein, contains a wealth of interesting examples of plant breeding in many

parts of the world but these are inaccessible because of an inadequate index. The figures are crude and some of the plates are either antiquated or of poor quality. G. HASKELL.

LYSENKO IS RIGHT. By James Fyfe. London : Lawrence & Wishart, 1950. Pp. 64. 2s. 6d.

" A botanist with 15 years' experience of agricultural plant breeding " explains how " the position taken by Lysenko and his followers is scientifically sound and fruitful in practice." The author is a member of the staff of the Cambridge Plant Breeding Institute.

THE SCIENCE OF HEREDITY. By J. S. D. Bacon. London : Watts (Thinker's Library), 1951. Pp. 192. 3s. 6d.

An account of genetics in simple language. Writing of the Lysenko controversy the author's opinion is : " The state of the controversy is therefore not very different in the Soviet Union from what it is in other countries." The author, who is Lecturer in Biochemistry at Sheffield University, acknowledges the help of Mr J. L. Fyfe.

GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers read at the HUNDRED AND FIFTH MEETING of the Society, held on TUESDAY, 20th MARCH 1951, at the GALTON LABORATORY, University College, Gower Street, London, W.C. 1

A COMBINATORIAL FORMULATION OF MULTIPLE LINKAGE TESTS

R. A. FISHER

Department of Genetics, Cambridge

Using a system of functions intimately related to the circular and hyperbolic functions of analysis, the expected frequencies of all observable modes of gamete formation may be expressed in terms of the metrical distances of the system of markers from each other and from the centromere and termini of the strand on which they lie.

KOSAMBI'S FORMULA GENERALISED FOR NON-ADJACENT SEGMENTS

A. R. G. OWEN

Department of Genetics, Cambridge

Kosambi's formula implies that the genetical coincidence for two adjacent segments 1 and 2 is given by $2y_1+2$. This assumption holds for segments not too near the centromere or the arm terminus and is useful because it enables the frequencies of modes of gamete formation with 3 linked loci to be expressed in terms of the two combination fractions y_1 and y_2, it necessarily fails when applied to three or four adjacent segments, for then we require a formula for the coincidence between two non-adjacent segments if the frequencies of modes of gamete formation are to be expressed in terms of segmental recombination fractions.

An appropriate generalisation has been found which is valid under the same conditions as Kosambi's formula.

GENETIC VARIANCE AND GENETIC CORRELATION IN PROGENY TESTS USING NON-RANDOM MATING

E. C. R. REEVE

Institute of Animal Genetics, Edinburgh

In tests to measure the heritabilities (h^2_w and h^2_t) and genetic correlation (r_g) of wing and thorax length (w and t) in *Drosophila*, flies were pair-mated and mean w and t of progeny from each mating measured. With random mating, the three parameters are estimated from the four regression coefficients of progeny on mid-parent dimension, but with high sampling variances.

More accurate estimates are obtained using a non-random mating system to increase mid-parent variance, *e.g.* phenotypic assortative mating or selection to increase parent variances. If such mating system is based on character w, the

regression of *w* and *t* progeny on *t* (but not on *w*) mid-parent are biased. Methods of eliminating the bias, assuming all the genetic variance is additive, are discussed. Appropriate corrections to the estimates based on sib-correlations are also available

If substantial non-additive genetic variance is present, non-random mating may bias all regressions, to an extent which depends on the gene frequencies and is very difficult to guess at. This problem deserves further study assuming different gene models.

MEASUREMENT OF PLEIOTROPIC EFFECTS IN PHENYLKETONURIA

L. S. PENROSE

Galton Laboratory, University College, London

Measurements of any given genetical effect can be expressed in terms of difference between means in normals and abnormals (D), divided by the mean standard deviation (S_1 and S_2)/2). Mean standard deviation is preferable to S, common standard deviation, when S_1 and S_2 are very unequal. In human genetics, imperfect segregation of genotypes is common and, for many characters, considered to be due to single genes. D/S lies between 2 and 4, *i.e.* between one in 6 and one in 40 individuals are wrongly classified.

The homozygous recessive phenylketonuric genotype is distinguishable in a variety of ways from the normal.

In phenylketonuria, D/S reaches a maximal value of 16 for the concentration of phenylalanine in the cerebro-spinal fluid ; for intelligence level, its value is about 6 and, for hair pigment dilution, it is less than unity. Since the same gene here has both major and minor effects, doubt is thrown on the usefulness of dividing genes into major and minor types.

Examples of similar results, obtained for characters due to other human genes and for sex, are discussed.

A LETHAL ALLELE OF DILUTE IN THE MOUSE

A. G. SEARLE

Department of Genetics, University College, London

A new mutant has appeared in the pure line C 57 Black. The gene, which is recessive, dilutes both yellow and black fur-colour. Pigment granules are clumped, as in Maltese dilution. Furthermore, the mutant suffers from neurological disorders of increasing severity, first appearing in the second week of life. When fully developed, these include violent convulsive fits with opisthotonus. The mutant rapidly loses weight and dies at about three weeks. Mating tests indicate that this lethal gene is an allelomorph of Maltese dilution, apparently completely recessive to it.

This is a further addition to the long list of pleiotropic genes in the mouse which affect fur-colour.

HETEROCARYOSIS IN WILD PENICILLIUM

J. L. JINKS

Genetics Department, Birmingham

Five examples of *P. assymetricum* group obtained from the wild, mostly as single spot infections on exposed plates, have given evidence of producing more than one genetical type of conidia, which in this species are uninucleate.

One colony, propagated by hyphal tips, was investigated more intensively. Thirty-four cultures were grown each from a single conidium. They could be divided into two groups, A and B, on the basis of growth rate on minimal medium. A grew faster than B but not so fast as the parent heterocaryon. They differed also in germination rate of their spores, but not in morphology. On complete medium the three growth rates were indistinguishable. Heterocaryons resembling the parent in growth rate were obtained by simultaneous inoculations of plates with pairs of spores, one from a monocaryon of type A and one from type B. Pairs of type A spores gave nothing but type A growth and pairs of B spores nothing but type B growth. On single sporing, these synthetic heterocaryons gave in their turn cultures of type A and type B in the same proportions as did the original. Thus the wild parent was a heterocaryon with two genetically different types of nucleus, which jointly give a higher growth rate than either did alone.

These results show that genetical variation exists in wild *Penicillium*; that heterocaryons are to be found in the wild; and that they can have an advantage over monocaryons, similar to the advantage which hybridity confers in wild outbreeding sexually reproducing species.

THE INFLUENCE OF LIGHT ON THE GERMINATION OF WATERCRESS SEEDS

W. H. HOWARD

Plant Breeding Institute, Cambridge

Seeds of *Nasturtium officinale* will germinate in both light and dark but seeds of *N. microphyllum* will only germinate in the light. Since seeds from the cross autotetraploid *N. officinale* female × *N. microphyllum* will only germinate in the light, it appears that the effect of light must be on the embryo and not on the testa, and that inability to germinate in the dark is dominant to ability. Results for the occasional seeds produced by the triploid hybrid *N. microphyllum* × *officinale* confirm these two conclusions. The results for two other types of seed, *N. microphyllum* female × *N. officinale* and amphidiploid *N. microphyllum-officinale* selfed, agree in showing that inability to germinate in the dark is dominant to ability. Similar results for light-needing v. indifferent seeds have been obtained by Honing (1830) in *Nicotiana*.

CONTRIBUTORS TO VOLUMES 1, 2, 3 AND 4

AUSTRALIA
- Burnett, F. M.
- Fenner, F.
- Montgomery, C.
- Smith-White, S.
- Walsh, R. J.

BELGIUM
- Heuts, M. J.

DENMARK
- Ditlevsen, E.
- Kemp, Tage
- Winge, Ø.

FINLAND
- Pesola, V. A.

FRANCE
- Ephrassi, B.
- L'Héritier, Ph.

GERMANY
- Pätau, K.
- Staudt, G.

INDIA
- Bhat, N. R.
- Majumdar, D. N.

ITALY
- Cavalli, L. L.
- Magni, G.
- Buzzati-Traverso, A.

JAPAN
- Kihara, H.

NEW ZEALAND
- Boyce, S. W.
- Copp, L. G. H.
- Frankel, O. H.
- Fraser, A. S.

NORWAY
- Berge, S.

PERU
- Harland, S. C.

SOUTH AFRICA
- Moffett, A. A.

SWEDEN
- Bonnier, G.
- Hansson, A.
- Müntzing, A.

TASMANIA
- Dobie, D. L.
- Ford, J. M.
- McAulay, A. L.

U.S.A.
- Dobzhansky, Th.
- Epling, C.
- Haskins, C. P.
- Haskins, E. F.
- Lederberg, J.
- Snell, G. D.

WEST INDIES
- Dodds, K. S.
- Simmonds, N. W.

UNITED KINGDOM
- Bateman, A. J.
- Billingham, R. E.
- Crane, M. B.
- Finney, D. J.
- Fisher, R. A.
- Ford, E. B.
- Koller, P. C.
- La Cour, L. F.
- Lewis, D.
- Mather, K.
- Medawar, P. B.
- Owen, A. R. G.
- Race, R. R.
- Yates, F.
- *and others*

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